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Limnological investigations:
Lake Koocanusa, Montana

Part 4: Factors controlling primary productivity

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P.F. Woods and C.M. Falter

FOREWORD

The Kootenai River basin, Libby Dam and the resulting Lake Koocanusa, have been of interest to CRREL investigators since the mid-1970's. We have focused on a number of cold regions remote sensing, water quality, and limnological problems. Of particular interest are those associated with winter ice cover, spring snowmelt runoff, and low temperature chemical reactions in sediments and in the water column. Since CRREL and the Seattle District have conducted a number of short and long term studies on the Kootenai River and Lake Koocanusa, we considered it appropriate to make the results of those investigations readily available in a series of reports. Therefore, we are issuing these results in the CRREL Special Report series under the overall title *Limnological investigations: Lake Koocanusa, Montana.*

Part 1: Pre-impoundment study: 1967–1972, with appendix, *Basic data*

Part 2: Environmental analyses in the Kootenai River region, Montana
(Reprint of CRREL Special Report 76-13)

Part 3: Basic data, post-impoundment: 1972–1978

Part 4: Factors controlling primary productivity
(CRREL Special Report 82-15)

Part 5: Phosphorus chemistry of sediments
(CRREL Special Report 81-15)

Cover: *Libby Dam and Lake Koocanusa, Montana,*
1975. (Photograph by U.S. Army Engineer
District, Seattle.)

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20. ABSTRACT *(Continue on reverse side if necessary and identify by block number)*

Postimpoundment loadings of total nitrogen and total phosphorus delivered to Lake Koocanusa by the principal inflowing stream, the Kootenai River, were predicted to be large enough to cause eutrophication of the lake; however, measured annual primary productivity for 1972 through 1975 was relatively low, and characteristic of oligotrophic waters. It was hypothesized that primary productivity was limited to oligotrophic values because phytoplankton photosynthesis was suppressed by physical limnological factors. The predominant flood-control function of the reservoir necessitates substantial reductions

20. Abstract (cont'd)

in volume during the autumn and winter. These large-scale water movements weakened the thermal structure of the reservoir. Thermoclines were often weakly developed and substantially deeper than the euphotic zone. A direct consequence of weak thermal structure was circulation of phytoplankton out of the euphotic zone which was important in suppressing annual primary productivity to oligotrophic levels. Circulation effects on photosynthesis were further compounded by highly turbid inflows. Euphotic zone depths were substantially reduced during filling, occasionally to less than 1 m. As a result, a large part of the phytoplankton population spent much of its time beneath the euphotic zone during this period. Nutrient limitation of phytoplankton photosynthesis was also suspected but not proven. The nonconformability of Lake Koocanusa to its predicted eutrophic response suggests that caution be used in applying nutrient loading models to reservoirs having complex hydrodynamics.

PREFACE

This report was prepared by P.F. Woods, former Graduate Research Assistant (present affiliation, U.S. Geological Survey, Water Resources Division, Anchorage, Alaska), and D. M. Falter, Professor of Fishery Resources, University of Idaho. The study was supported by the Seattle District, U.S. Army Corps of Engineers, under contract DACW67-76-C-0087. Publication of this report is in conjunction with the Corps of Engineers Civil Works Program, Environmental Quality, Work Unit 31013 Environmental Effects and Criteria for Engineering. Works in Cold Regions.

The authors express their appreciation to T. Bonde and R. Bush, U.S. Army Engineer District, Seattle, for their assistance in providing data and consultation. This report was technically reviewed by T. Bonde, R. Bush, and P. Storm, Environmental Resources Section, U.S. Army Engineer District, Seattle, and Dr. J. E. Hobbie, CRREL Consultant, Marine Biological Laboratory, Woods Hole, Massachusetts.

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INTRODUCTION

Libby Dam and its resultant reservoir, Lake Koocanusa, were con-
structed on the Kootenai River (spelled Kootenay in Canada) as part of a
treaty between the United States and Canada for cooperative development
of the water resources of the Columbia River Basin. Lake Koocanusa was
impounded on 21 March 1972 to provide flood storage, hydroelectric
power, and recreation.

Preimpoundment water quality studies conducted since 1967 predicted
that annual loadings of total nitrogen (N) and total phosphorus (P) per
square meter of reservoir surface would be 20 and 10 g, respectively; 4
and 10 times the values that could cause eutrophication of Lake Koocanusa
(Bonde and Bush 1975). Blooms of _Aphanizomenon_ _flos-aquae_, a blue-green
algae characteristic of eutrophic waters, occurred in the reservoir
during the autumns of 1974 and 1975.

Postimpoundment water quality studies have been conducted yearly
since 1972. Preliminary evaluations of this information revealed that
primary productivity was predominantly controlled by physical limnolog-
ical factors (Hobbie 1975, Bush and Bonde 1977). Woods (1979) reported
that primary productivity in Lake Koocanusa during 1972-1975 was charac-
teristic of oligotrophic, not eutrophic, waters.

To better understand the aquatic environment of the reservoir, the
postimpoundment water quality data were thoroughly evaluated. The U.S.
Army Corps of Engineers had the Fishery Resources Department of the
University of Idaho evaluate these data collected from 1972 (impound-
ment) through 1975. This report evaluates the physical, chemical, and
biological properties that controlled primary productivity in Lake
Koocanusa from 1972 through 1975.

KOOTENAI RIVER DRAINAGE BASIN

Characteristics of the Kootenai River drainage basin have been
described by Bonde and Bush (1975) and Water Resources Services (1976)
and only those pertinent to that part of the drainage basin influencing
Lake Koocanusa will be summarized here.
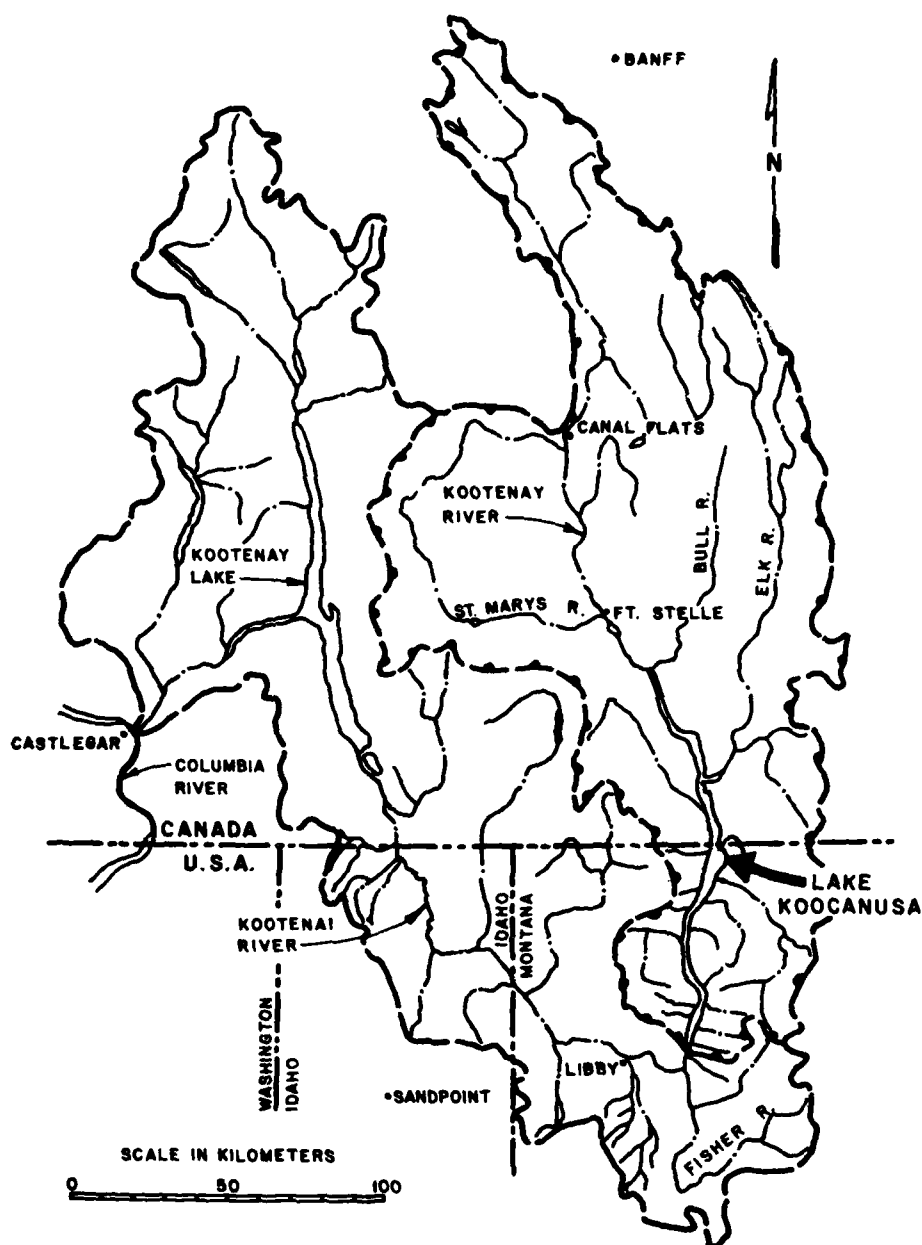
Figure 1. Kootenai River (spelled Kootenay in Canada) drainage basin.

Lake Koocanusa and its tributaries receive drainage from 23,271 km^2 or 47% of the Kootenai River drainage basin (Fig. 1). The basin lies between $48°$ and $51°$ north latitude and $115°$ and $118°$ west longitude. The Kootenai River, the principal tributary to Lake Koocanusa, arises near Banff, British Columbia, and flows southward for 161 km before entering the Rocky Mountain Trench near Canal Flats, British
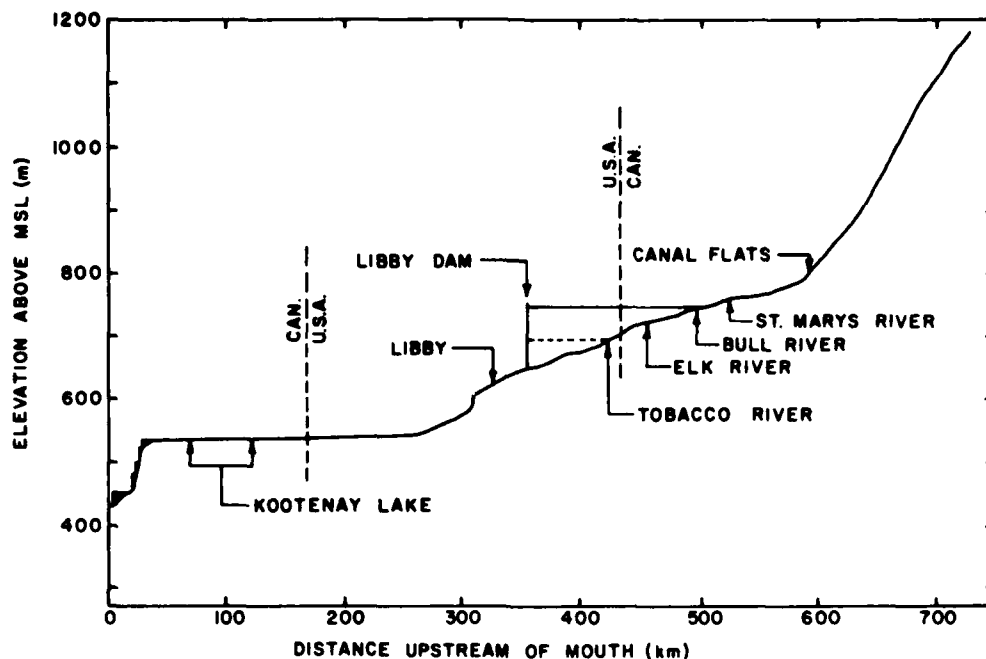
Figure 2. Longitudinal profile of the Kootenai River.

Columbia. The Rocky Mountain Trench is a broad valley underlain with thick (457 to 1372 m) deposits of sedimentary and glacial origin (Water Resources Services 1976). The river continues south for another 161 km, then leaves the Rocky Mountain Trench and enters the United States to flow southward through the Purcell Mountains for 80 km to its confluence with the Fisher River. Libby Dam spans the Kootenai River at a point 4.5 km upstream of the Fisher River. The Kootenai River then flows west across northern Idaho, entering Kootenay Lake in British Columbia and finally the Columbia River near Castlegar, British Columbia. The Kootenai River, 780 km in length, begins at an elevation of about 1200 m above mean sea level (m.s.l.) and enters the Columbia River at 418 m above m.s.l. (Fig. 2).

The drainage basin is located within the Northern Rocky Mountain physiographic province, which is characterized by north to northwest trending mountain ranges separated by straight valleys parallel to the ranges. These mountains are composed of folded and faulted crystal blocks of metamorphosed sedimentary rocks of the Precambrian Belt Series.

The Rocky Mountain Trench annually receives an average of 400 mm of precipitation. The Rocky and Purcell Mountains annually receive an

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average of 1000 mm and 1000 to 1500 mm of precipitation respectively.
Libby, Montana, has received an annual average of 469.1 mm of precipi-
tation since 1895 (U.S. Department of Commerce 1972, 1973, 1974, 1975).
At Libby, the annual precipitation for 1972, 1973, 1974 and 1975 was,
respectively, 104, 76, 98 and 112% of the historic average. Snow,
representing 70% of the annual precipitation, falls from November to
March. Mean air temperatures in the Rocky Mountain Trench are 18° C
in July and about -10° C in January. About 75% of the winter days and
50% of the summer days are cloudy.

Cultural and industrial development is sparse within the drainage
basin upstream from Libby Dam. The principal industries are forestry,
mining, agriculture and tourism. Some of these activities create point
and nonpoint sources of water pollution potentially degrading to the
water quality of Lake Koocanusa.

Major municipal point sources of water pollution are from Cranbrook
and Kimberly, British Columbia, and Eureka, Montana. Industrial point
source discharges are from an underground mine and ore concentrator
facility, a phosphate fertilizer plant at Kimberley, and a bleached
kraft pulp mill near Skookumchuk. Cominco Ltd. operates the Sullivan
Mine and its ore concentrator, one of the world's largest lead and zinc
mining facilities. This facility has discharged largely untreated
effluents with high concentrations of heavy metals to tributaries of the
St. Marys River. Cominco Ltd. also operates the phosphate fertilizer
plant at Kimberley. The largely untreated 9 million gallons per day
(mgd) of effluent, high in dissolved fluoride, iron, lead and total P,
was discharged to a tributary of the St. Marys River. Crestbrook Forest
Industries Ltd. discharged 11 mgd of effluent from its bleached kraft
pulp mill. Prior to discharge, the effluent was treated in a settling
and aeration pond. These three industrial point sources continued dis-
charges from 1972 through 1975, the period of data collection at Lake
Koocanusa.

Nonpoint water pollution comes from agriculture in the Rocky Moun-
tain Trench and timber harvesting in the coniferous forests covering
much of the drainage basin. Croplands and livestock ranching yielded
small annual loadings of N and P but have not caused measurable deteri-
oration of water quality in the Kootenai River upstream of Lake Koocanusa
(Water Resources Services 1976). The impact of timber harvesting within

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the drainage basin has not been assessed but it probably increases sedi-
mentation (Water Resources Services 1976).

DATA BASE

Water quality data from the cooperative studies by the U.S. Army
Corps of Engineers and British Columbia Ministry of the Environment,
Waste Management Branch (formerly Pollution Control Branch), were com-
piled and analyzed for four United States reservoir stations, four
Canadian reservoir stations (Fig. 3), the Kootenai River 1.1 km down-
stream of Libby Dam, and the Canadian tributaries to Lake Koocanusa.
Streamflow values and portions of the water quality data for the United
States have been published by the U.S. Geological Survey (1973a, 1974a,
1975a, 1976, and 1977) and are filed in both the U.S. Geological Survey
WATSTORE system and the Environmental Protection Agency STORET system.
The Canadian water quality data are filed in the British Columbia Minis-
try of the Environment EQUIS system. Canadian streamflow data have been
published by the Inland Waters Directorate (1973, 1974, 1975, and 1976).

Vertical profiles of water temperature, specific conductance, dis-
solved oxygen and pH were measured in situ with a multiprobe water
quality analyzer (Martek Co.). A transmissometer was used to obtain
vertical profiles of in situ percent light transmission. Percent light
transmissions were converted to vertical extinction coefficients with
the following equation:

$$\eta = \ln \left(\frac{P}{T \times 0.01} \right)$$

where η is vertical extinction coefficient, P is light path length in
meters and T is percent light transmission.

Vertical profile data were processed into isopleth diagrams using a
package of computer programs titled STAMPEDE (Surface Techniques, Anno-
tation, and Mapping Programs for Exploration, Development, and Engineer-
ing) (IBM program no. 300-17.4.001). The programs in the STAMPEDE
package were used to numerically describe each set of water quality
parameters as x (date), y (depth), and z (parameter value) data points
on a grid. Contour lines were then produced from the numerical grids
and output on an off-line plotting device. Symbols representing the
date of the initial vertical profile and the final vertical profile were
plotted on each isopleth diagram. In general, vertical profiles were

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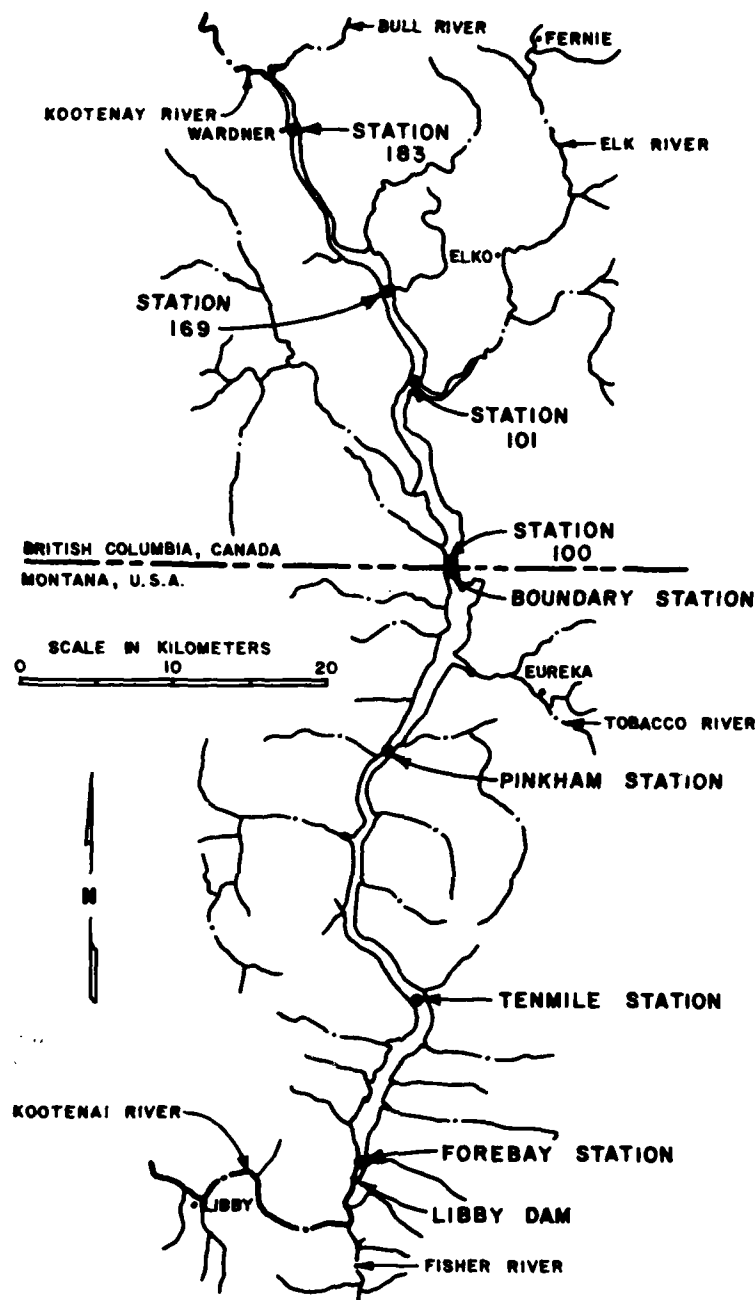
Figure 3. Sampling stations and principal tributaries
of Lake Koocanusa.

made on a weekly or biweekly schedule during the sampling season.

Major and minor chemical constituents were sampled at 3.1 m below
the surface and 3.1 m above the reservoir's bottom. Chemical deter-
minations were made according to Brown et al. (1970) and Goerlitz and

Table 1. Watershed export coefficients to determine annual inputs in $g\ m^{-2}$ yr^{-1} of total P and total N (after Rast and Lee 1978).

	Total P	Total N
Forested land	0.01	0.1
Direct precipitation	0.02	0.8
Dry fallout	0.08	1.6

Brown (1972). Beginning in July 1974 chlorophylls 'a' and 'b,' uncorrected for phaeopigments, within the euphotic zone were measured according to Goerlitz and Brown (1972). In situ primary productivity was determined according to methods of Janzer et al. (1973).

Daily loadings of total P and total N were calculated with the following equation:

$$L = C \times Q \times f$$

where L is loading in metric tons per day, C is nutrient concentration in $mg\ L^{-1}$, Q is mean daily streamflow in $m^3\ s^{-1}$, and f is 0.0000864, a factor to convert units into metric tons per day. Annual loadings were summations of daily loadings. Measured nutrient concentrations were linearly interpolated to obtain estimated daily concentrations. Influent stream loadings were determined for the Kootenay, Elk, and Bull Rivers. Loadings discharged from Lake Koocanusa were determined for the Kootenai River immediately downstream of Libby Dam. Inputs of total P and total N from the 6022 km^2 area not included in the gauged drainage areas of the Kootenay, Elk, and Bull Rivers were estimated with watershed export coefficients. Rast and Lee (1978) cited watershed export coefficients for estimating the annual inputs from forested areas, direct precipitation, and dry fallout (Table 1). Mean annual reservoir surface areas of 95.1 km^2 (1972-73) and 135.6 km^2 (1974-75) were used as catchment areas for calculating direct precipitation and dry fallout. Contributions of total P and total N from groundwater were not quantifiable.

Table 2. Volume, surface area, and mean depth of Lake Koocanusa at various reservoir surface elevations.

Surface elevation (m)	Volume (km^3)	Maximum volume (%)	Surface area (km^2)	Maximum area (%)	Mean depth (m)
749.50*	7.16	100.0	188.2	100.0	38.1
740.00	5.52	77.1	159.4	84.7	34.6
730.00	4.08	57.0	131.5	69.9	31.0
720.00	2.91	40.6	103.2	54.8	28.2
710.00	1.99	27.8	80.9	43.0	24.6
700.00	1.26	17.6	64.8	34.4	19.5
697.08+	1.08	15.1	59.1	31.4	18.3
690.00	0.71	9.9	46.5	24.7	15.2
680.00	0.34	4.7	27.5	14.6	12.5
671.17**	0.14	2.0	16.2	8.6	8.6

* Maximum pool.

+ Minimum operational pool.

** Dead storage.

PHYSICAL LIMNOLOGY

Morphometrics

For flood control Lake Koocanusa's volume must be substantially reduced during the fall and winter to provide adequate capacity to hold the spring snowmelt runoff. This schedule causes a number of changes in the reservoir's morphometry (Table 2). At full pool the reservoir is 148 km in length, has a volume of 7.16 km^3, and a surface area of 188 km^2. Drawdown to the minimum operational pool reduces the length of the reservoir to 67.6 km, the volume to 1.08 km^3, and the surface area to 59.1 km^2. The surface elevation at full pool is 749.50 m above m.s.l., and the minimum operational pool is at 697.08 m above
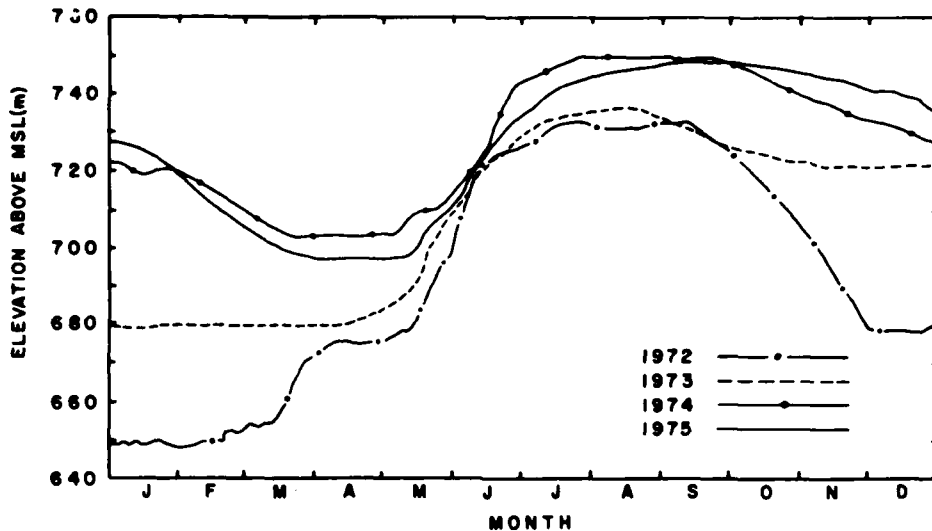
Figure 4. Lake Koocanusa's surface elevations, 1972 through 1975.

m.s.l. The dead storage capacity of 0.14 km^3 lies below an elevation
of 671.17 m above m.s.l. At full pool the reservoir has a maximum depth
of 107 m.

Libby Dam is a concrete gravity structure with three types of out-
lets: three sluiceways with invert elevations at 671.17 m above m.s.l.,
four operational penstock intakes (eight ultimately) with invert eleva-
tions of 677.27 m above m.s.l., and a gated spillway with an invert
elevation of 733.04 m above m.s.l.

Water budget

The fluctuations in reservoir surface elevation from initial impound-
ment through 1975 reflected the differing rates of inflow and outflow
(Fig. 4). Inflow was calculated from the change in the water content of
the reservoir. Change in content was used as the best available esti-
mate of influent streamflow because complete streamflow records were
available only for the Kootenai, Bull, Elk and Tobacco rivers. The mean
monthly inflow was highest during May, June and July (Fig. 5). The mean
monthly outflow, measured 1.1 km downstream of Libby Dam, is also graphed
in Figure 5.

Mean annual (calendar year) discharges from Libby Dam were as
follows: 1972, 424.2 m^3s^{-1}; 1973, 178.5 m^3s^{-1}; 1974, 420.6 m^3s^{-1};
and 1975, 288.3 m^3s^{-1}. A stream gauging station at Libby, 28.3 km
downstream from Libby Dam, has recorded streamflow since 1910. Compared

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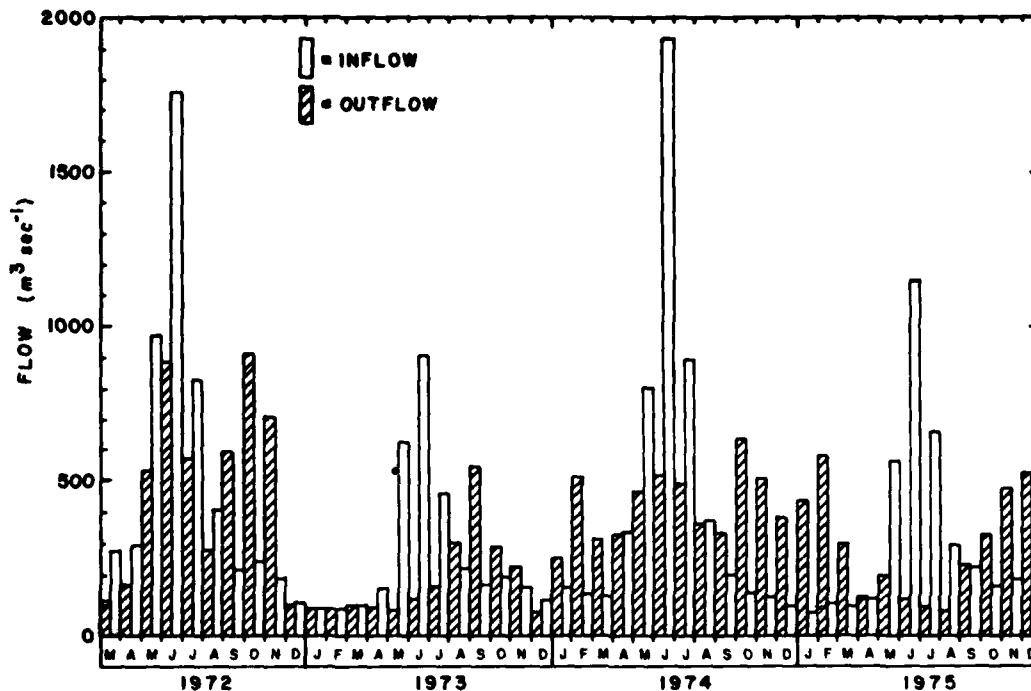
Figure 5. Mean monthly inflow and outflow of Lake Koocanusa, 1972 through 1975.

Table 3. Historic and postimpoundment mean annual discharges of the Kootenai River at Libby, Montana.

Calendar year	Mean annual discharge ($m^3 s^{-1}$)	Percent of historical discharge
1972	458.8	133
1973	189.6	55
1974	465.0	135
1975	321.7	93
1910-1972	344.6	—

to the historic mean annual discharge, mean annual discharge at Libby was above average in 1972 and 1974, about average in 1975, and below average in 1973 (Table 3). The sluiceways handled the discharge from 1972 through 1975 except for those periods when the spillway was used,

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August through early November 1974 and July 1975. Hydroelectric power was first generated via the penstocks on 12 August 1975 and since then has been nearly continuous.

Retention and flushing time

The relationship between the volume of a reservoir and the inflow volume per unit time has been variously termed detention time, bulk residence time, renewal time, basin filling time and, as used in this report, retention time. Retention time is the average time required to replace the contents of a reservoir at a given rate of inflow. A mean retention time of 0.67 years was calculated for Lake Koocanusa, based on mean annual volume and annual flow (Bush and Bonde 1977). Because of the reservoir's wide range of volumes, retention times calculated for this report were derived for each month by the following equation:

$$RT = \frac{V}{I} \times 0.0833$$

where RT is retention time in years, V is mean volume in m^3, I is total monthly inflow in m^3, and 0.0833 is the conversion of months to years.

The importance of flushing time (volume/outflow) to the potential trophic status of a water body was established by Dillon (1975) and Larsen and Mercier (1976). Flushing time is defined here as the average time required to remove the reservoir's contents at a given outflow rate. Flushing time for each month was calculated in the same manner as was retention time except that outflow was substituted for inflow. Mean monthly retention and flushing times are presented in Table 4.

Water temperature

Water temperatures in Lake Koocanusa ranged from 1° to 23° C; the maximum surface temperatures are found in late July or early August (Appendix A, Fig. A1 through A4). Surface cooling and subsequent upper level circulation commenced in mid to late August. Isothermy occurred later at the Forebay and Tenmile stations than at the Pinkham and Boundary stations.

The mean monthly temperatures of water released from Libby Dam

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Table 4. Mean monthly retention and flushing times of Lake Koocanusa, 1972-1975.

	1972	1973	1974	1975
Retention time (yr)				
Mean	0.20	0.39	0.66	0.68
SD	0.19	0.33	0.52	0.45
Minimum	0.02	0.04	0.06	0.08
Maximum	0.61	0.84	1.43	1.40
No. of observations	9	12	12	12
Flushing time (yr)				
Mean	0.14	0.45	0.32	0.73
SD	0.11	0.37	0.19	0.77
Minimum	0.04	0.11	0.13	0.12
Maximum	0.36	1.26	0.70	2.55
No. of observations	9	12	12	12

varied from near 0° to 16.0° C, as measured by a continuous recording thermograph located 1.1 km downstream of the dam (however, data were generally not available from December through March) (Fig. 6). The water temperatures peaked in August and September of 1974 and July of 1975 when surface water was discharged through the spillway in place of cooler water normally discharged through the sluiceways. Maximum daily water temperatures recorded by the thermograph were 14.5°, 14.5°, 17.0° and 19.5° C for September and October of 1972, October of 1973, August and September of 1974 and July and August of 1975 respectively.

The wide spacing of isotherms in Figures A1 through A4 indicates a predominantly weak thermal structure. In order to quantify the reservoir's thermal structure, vertical stability gradients, representing the resistance of a small mass of water to turbulent mixing, were calculated using vertical profiles of water temperature. The theoretical basis of vertical stability has been discussed by Heitman (1973). When a small mass of water is displaced vertically upward from an initial depth Z_1

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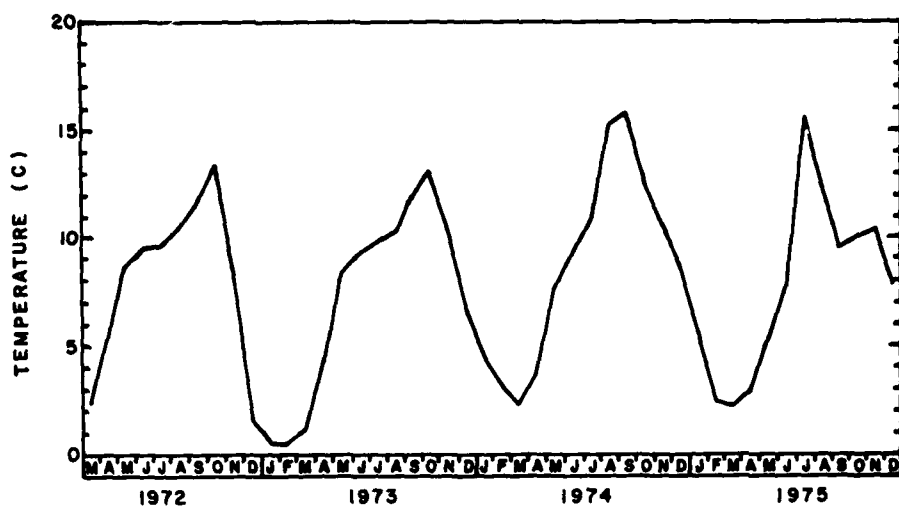
Figure 6. Monthly mean temperatures (°C) of water released from Libby Dam, measured once daily, 1972 through 1975.

to a new depth Z_2 it will possess density p_1 at depth Z_2 and the surrounding water at depth Z_2 will possess density p_2. If the density difference is positive, the displaced water mass moves back toward the original depth Z_1 and equilibrium conditions are considered stable. If the density difference is negative, equilibrium conditions are unstable and the water mass moves away from the original depth Z_1. Neutral equilibrium exists when the density difference is zero.

A measure of the state of equilibrium is the density difference per unit length. Vertical stability gradients were calculated with the following equation:

$$E = \frac{P_1 - P_2}{Z_2 - Z_1} \times \frac{1 \text{ m}}{100 \text{ cm}}$$

where E is vertical stability gradient in g cm^{-2}, p_1 is density in g cm^{-2} of displaced water mass, p_2 is density in g cm^{-2} of surrounding water, Z_1 is elevation in meters from which water mass was displaced, and Z_2 is elevation in meters to which the water mass was displaced.

The stratum with the largest vertical stability gradient was taken as the thermocline, the lower boundary of the epilimnion. The thermocline has often been arbitrarily designated as the region in which the temperature gradient exceeds $1°$ C m^{-1}; however, Hutchinson (1957)

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defines the thermocline as the stratum with the maximum rate of temperature decline. Relative stabilities were computed to contrast measured vertical stability gradients with those vertical stability gradients with a change of 1° C m^{-1}. For example, if a measured vertical stability gradient of 3.51×10^{-5} g cm^{-2} represented a temperature decline from 10.2° to 9.8° C, the vertical stability gradient associated with a temperature decline from 10.5° to 9.5° C would be 8.79×10^{-5} g cm^{-2}. The relative stability would therefore be 40% (3.51×10^{-5} / 8.79×10^{-5} x 100). Of the 145 relative stabilities computed for Lake Koocanusa during 1972 through 1975, only 27, or 18.6% of those measured, were equal to or greater than 100% (Table 5). The largest relative stabilities generally occurred in July and August. The vertical stability gradient calculations revealed the existence of secondary and multiple thermoclines above the primary thermocline. Such secondary and multiple thermoclines were transitory because of the turbulence present in the upper water column.

Turbulence in the upper water column is primarily generated by Langmuir circulation (Faller 1969, Harris and Lott 1973a). Langmuir circulation is a series of parallel, counter-rotating cells that produce zones of upwelling and downwelling. Downwelling current velocities were found to be directly proportional to windspeed; winds of 3 and 9 m s^{-1} produced downwelling velocities of about 2.5 and 7.5 cm s^{-1} respectively (Scott et al. 1969). Langmuir circulation is active at wind speeds greater than 2 to 3 m s^{-1} and is often evidenced by parallel surface slicks; however, Langmuir circulation can exist without these slicks (Faller 1969). Lake Koocanusa is frequently windy and often bears the characteristic surface slicks of Langmuir circulation (Bonde, pers. comm.).

The depth to which wind-induced turbulence penetrates largely depends upon wind stress and the thermal structure of the upper water column (Scott et al. 1969). Under well-stratified conditions, the thermocline is the lower boundary of turbulent mixing, but with weak or absent stratification turbulent mixing may penetrate deeply into the water column.

The weak thermal structure of Lake Koocanusa was largely attributable to the complexity of water movements within the reservoir. Water

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Table 5. Relative stability of stratification from 1972-1975 at four
reservoir stations.

Date	Relative stability (%)			
	Boundary	Pinkham	Tenmile	Forebay
1972				
July	127	41	51	104
August	44	41	71	103
September	242	21	33	15
October	246	48	32	24
November	--	0	1	0
1973				
April	--	--	35	0
May	--	0	55	21
June	48	28	39	17
July	133	139	294	156
August	75	75	74	119
September	47	--	41	34
October	122	90	31	31
November	--	0	42	29
1974				
April	--	57	0	0
May	--	0	0	41
June	41	13	43	186
	418	--	259	111
July	83	55	48	27
	119	69	47	242
August	132	181	124	54
	36	64	63	98
September	82	112	72	82
	59	55	69	68
October	24	35	42	49
	25	0	28	13
	43	0	17	--
November	--	--	0	14
	--	--	--	0
1975				
April	--	--	0	0
May	--	--	50	0
	--	0	46	70
June	0	0	143	50
	0	27	39	55
July	54	112	135	40
	125	100	101	54
August	96	165	89	75
	88	75	64	63
September	69	49	42	31
	2u	34	56	49
October	27	33	42	23
	0	0	28	28

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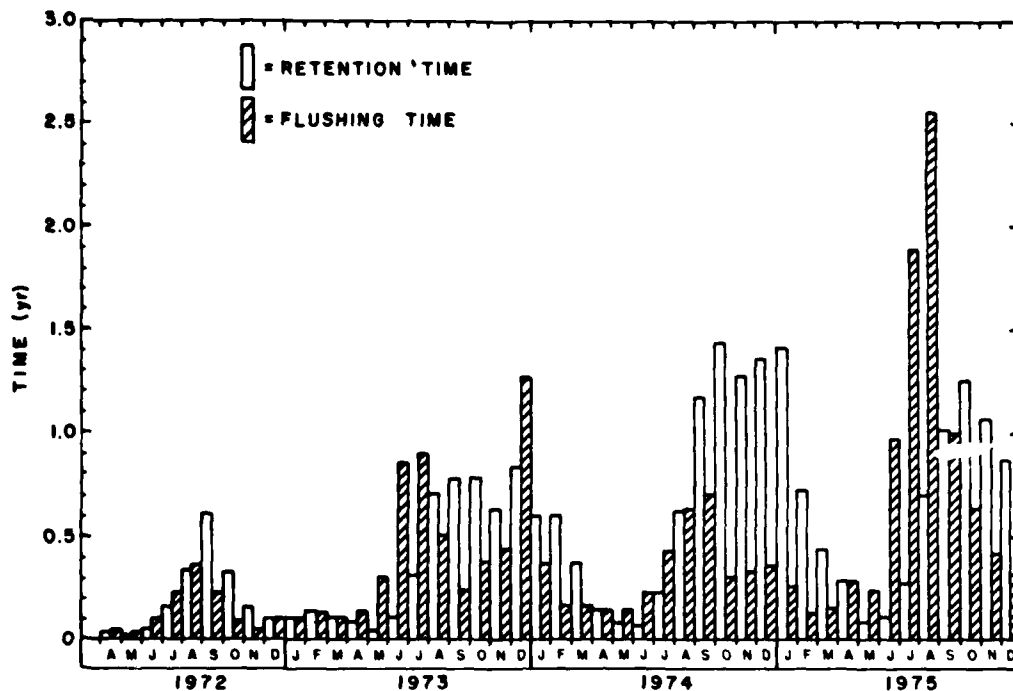
Figure 7. Monthly retention and flushing times for Lake Koocanusa, 1972 through 1975.

movements in reservoirs result from the interactions of currents, thermal stratification, basin morphology and climate, and reservoir operations. The unsteady nature of inflow and outflow currents largely accounts for the continual water movement present in many reservoirs (Wunderlich 1971). Currents generated by large volumes of inflow and outflow drive lateral advective heat transport and, by turbulence induction, vertical advection heat transport. The magnitude of the turbulence induced by inflow and outflow currents is due in part to the relative volumes of inflow and outflow, and reservoir volume. When flows are large relative to reservoir volume, retention times (volume/inflow) or flushing times (volume/outflow) will be reduced. Retention and flushing times varied widely in Lake Koocanusa (Fig. 7). In each of the 4 years, retention times were less than 0.1 years as large volumes of spring runoff entered the drawdown reservoir. Flushing times were also short during reservoir filling and drawdown. In general, short retention and flushing times were associated with weak thermal structure. Schraeder, as cited by Straskraba (1973) reported that the thermal structures of reservoirs in Thuringer Wald were affected by retention

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time because large inflows reduced thermal gradients. Thermal structure may also be modified by heat advection caused by outflow currents (Wunderlich 1971).

Light

Once light has passed through a water surface, it is attenuated by scattering and absorption. Attenuation is exponential, as shown by the following equation:

$$I_z = I_0 e^{-\eta Z}$$

where I_z is the light intensity at the upper stratum, I_0 is the light intensity at the lower stratum, e is the base of the natural logarithm, Z is the depth difference in meters between strata, and η is the extinction coefficient. The extinction coefficient is a composite of absorption by water, and scattering by suspended particles and dissolved compounds. Extinction coefficients may be 0.2 in very clear lakes, 4.0 in lakes with high levels of biogenic turbidity and greater than 10.0 in reservoirs with extremely turbid inflows (Wetzel 1975).

Historically, the Kootenai River has carried large loadings of suspended sediment during spring runoff (Bonde and Bush 1975). Because of this, the reservoir contained very turbid water during filling, as evidenced by isopleth diagrams of extinction coefficients for 1973 through 1975; data were not available for 1972 (Fig. B1 through B3). High extinction coefficients were distributed uniformly with depth at the Pinkham and Boundary stations, which were relatively shallow and near the upstream end of the reservoir. High extinction coefficients at the two downstream stations, Tenmile and Forebay, tended to be concentrated well below the surface. Although the suspended sediment settled rapidly, extinction coefficients greater than 4.0 generally persisted in near-surface water from the start of filling through June or July.

Euphotic zone depth, defined here as the depth at which light intensity is 1% of that incident to the surface, varied from less than 1 to 18 m. The shallowest depths were measured during reservoir filling (Fig. 8). The Boundary and Pinkham stations were extremely turbid during filling because they received the sediment normally carried by the Kootenai River, in addition to resuspended sediments from the upstream reservoir that were exposed by drawdown. The Boundary station was exposed by drawdown until about mid-May in each of the 4 years and the Pinkham station was exposed through early May of 1972 and 1973.

17
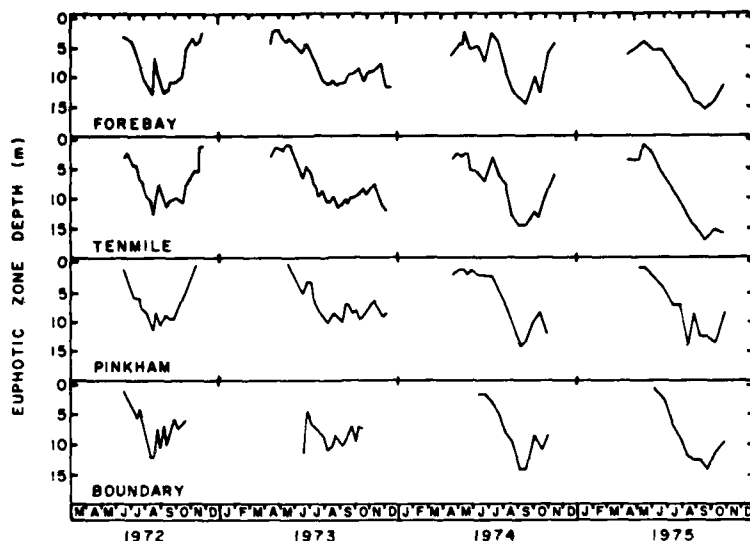
Figure 8. Euphotic zone depths at four U.S. reservoir
stations, 1972 through 1975.

Suspended sediment

In addition to its impact on reservoir extinction coefficients, sus-
pended sediment discharged through Libby Dam affected riverine turbidity.
Reservoirs generally function as sediment traps and reduce loadings of
suspended sediment downstream from a dam, and such was the case for the
Kootenai River downstream of Libby Dam. Suspended sediment data sum-
marized in Table 6 indicate a substantial reduction in loadings follow-
ing impoundment in March of 1972. Mean and maximum turbidity values in
the Kootenai River just downstream of Libby Dam also declined substan-
tially following impoundment (Table 7).

NITROGEN AND PHOSPHORUS

A large number of chemical constituents were sampled at Lake Koocan-
usa and the Kootenai River immediately downstream of Libby Dam. N and P
data will be discussed in more detail because of concern over the large
loadings to Lake Koocanusa of these two algal nutrients.

Loadings of N and P

Based on the premise that stream loadings of N and P during 1969-
1971 would be representative of postimpoundment loadings, Bonde and Bush
(1975) predicted that 3000 metric tons of total N and 2000 metric tons

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Table 6. Loading of suspended sediment in the Kootenai River (metric tons) measured within 6 km downstream of Libby Dam site.

Year	Yearly total	Monthly mean	Monthly maximum	Monthly minimum
1968	1,413,076	117,756	905,167	2,642
1969	2,425,036	202,086	1,112,709	995
1970	429,567	35,797	257,870	643
1971	1,562,913	130,243	856,718	1,295
1972	166,476	13,873	67,922	643
1973	29,910	2,493	7,616	560
1974	77,754	6,480	17,610	2,519
1975	117,017	9,751	58,579	864

Table 7. Turbidity (JTU) measured in the Kootenai River between the Libby Dam site and a point 6 km downstream.

Period	Mean	Maximum	Minimum	n
1970	9.0	58	1	12
1971	13.1	75	1	12
1972	10.9	50	1	44
1973	3.7	9	1	52
1974	3.1	17	1	36
1975	3.0	8	1	25

of total P would be delivered annually to Lake Koocanusa. Following impoundment, the annual loadings of total N delivered to Lake Koocanusa during 1972-1975 ranged from 2180 to 3330 metric tons (X (mean) = 2761.0, standard deviation (S.D.) = 599.4, number of observations (n) = 4). The range of annual loadings of total P during 1972-1975 was 1002 to 1636 metric tons (X = 1448.3, S.D. = 302.1, n = 4). The largest loadings of total N and total P were observed during spring runoff when the reservoir was refilling (Table 8).

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Table 8. Loadings in metric tons of total P (TP) and total N (TN) delivered to Lake Koocanusa, 1972-1975.

	1972*		1973		1974		1975	
	TP	TN	TP	TN	TP	TN	TP	TN
Stream loadings								
January	--	--	61.4	88.2	32.0	95.2	50.6	41.5
February	--	--	78.9	73.5	108.6	47.3	60.6	38.9
March	23.3	44.8	77.1	65.8	127.3	81.6	67.5	48.1
April	47.3	111.8	80.0	57.8	72.8	185.2	66.2	57.9
May	247.1	628.0	437.8	309.7	293.1	455.5	255.1	372.6
June	242.5	916.6	393.4	463.9	651.3	1139.2	542.7	749.0
July	73.5	298.3	83.0	261.8	213.2	517.0	184.5	278.0
August	44.3	162.6	32.1	132.9	48.1	176.4	63.3	111.0
September	66.4	414.4	43.1	88.2	8.9	76.8	64.0	63.5
October	61.7	406.1	77.7	72.2	4.6	38.4	104.8	44.4
November	39.7	86.4	212.5	112.4	11.3	29.7	25.4	67.5
December	48.6	76.8	48.8	216.7	48.3	40.7	20.3	98.4
Total	994.4	3145.8	1625.8	1943.1	1619.5	2883.0	1505.0	1970.8
Other loadings								
Forest drainage	0.7	7.4	1.0	9.5	1.4	13.6	1.4	13.6
Dry fallout	5.9	118.7	7.6	152.2	10.8	216.9	10.8	216.9
Precipitation	1.5	59.4	1.9	76.1	2.7	108.5	2.7	108.5
Total	8.1	185.5	10.5	237.8	14.9	339.0	14.9	339 0
Total loading	1002.5	3331.3	1636.3	2180.9	1634.4	3222.0	1519.9	2309.8

*Data for March 21 through December 31.

Table 9. Loadings in metric tons of total P (TP) and total N (TN) delivered to the Kootenai River downstream of Libby Dam, 1972-1975.

	1972*		1973		1974		1975	
	TP	TN	TP	TN	TP	TN	TP	TN
Stream loadings								
January	--	--	40.6	125.3	45.9	202.2	22.7	295.8
February	--	--	39.9	105.0	72.8	337.5	18.1	207.8
March	7.4	43.1	57.6	136.5	52.7	244.7	18.0	237.0
April	37.8	139.0	38.2	94.3	78.6	319.7	11.7	78.3
May	176.1	420.4	16.6	42.6	115.2	370.2	17.0	140.7
June	251.9	640.9	23.0	84.0	88.0	446.9	12.1	74.6
July	110.0	357.4	20.6	185.9	67.3	242.2	10.9	53.1
August	47.4	333.3	45.2	277.8	44.9	206.0	7.8	52.7
September	67.8	419.9	93.4	286.7	16.7	210.4	34.4	235.6
October	103.9	593.2	95.7	195.3	40.4	408.6	57.4	159.4
November	89.9	425.2	56.4	141.8	44.8	183.4	55.8	911.5
December	20.4	139.8	21.6	61.6	15.6	255.5	53.9	279.3
Total	912.6	3512.2	548.8	1736.8	682.9	3427.3	319.8	2725.8

*Data for March 21 through December 31.

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Annual loadings of total N and total P discharged into the Kootenai River immediately downstream of Libby Dam during 1972-1975 ranged from 1736 to 3512 metric tons of N ($X = 2850.5$, S.D. = 821.9, n = 4) and from 320 to 913 metric tons of P ($X = 616.0$, S.D. = 248.1, n = 4). The largest monthly loadings of total N generally were found while the reservoir was drawndown, whereas monthly loadings of total P reached their largest values while the reservoir was filling in 1972 and 1974 and while it was being drawndown in 1973 and 1975 (Table 9). Annual loadings of total N and total P during 1971 at a point 6 km downstream of Libby Dam were, respectively, 4057 and 1924 metric tons (Bonde and Bush 1975). When compared to these preimpoundment values, the mean annual loadings for 1972-1975 indicate that Lake Koocanusa has sharply reduced the total N and total P annually delivered into the Kootenai River immediately downstream of Libby Dam.

The fate of influent loadings to reservoirs can be assessed with nutrient retention coefficients (Rast and Lee 1978). Nutrient retention coefficients were calculated with the following equation and are summarized in Table 10:

$$R = 1 - \frac{EL}{IL}$$

where R is the nutrient retention coefficient, EL is effluent loading in metric tons per unit time, and IL is influent loading in metric tons per unit time. Monthly retention coefficients for both nutrients were positive and large while the reservoir was filling. During drawdown, a period when there is much more outflow than inflow, both nutrients had negative retention coefficients, indicating nutrient removal from the reservoir. Total N had negative retention coefficients for most months. On a yearly basis, the reservoir retained most of its P loadings and essentially none of its N loadings.

The retention of total P is partly attributable to transport and sedimentation of clay-bound P into Lake Koocanusa. Phosphorus is readily adsorbed to clay minerals, nitrate is not (Lee 1970). The Kootenai River upstream of Lake Koocanusa traverses deep sedimentary and glacial deposits containing clays and silts (Crozier and Leinweber 1975).

The inflow characteristics of Lake Koocanusa also accounted for the high retention of total P. At the point of inflow into a reservoir, there generally is rapid mixing of riverine and reservoir water. As

Table 10. Monthly and annual retention coefficients of total P (TP) and total N (TN) in Lake Koocanusa, 1972-1975.

	1972		1973		1974		1975	
	TP	TN	TP	TN	TP	TN	TP	TN
January	--	--	0.34	-0.42	-0.43	-1.12	0.55	-6.13
February	--	--	0.49	-0.43	0.33	-6.14	0.70	-4.34
March	0.68	0.04	0.25	-1.07	0.59	-2.00	0.73	-3.93
April	0.20	-0.24	0.52	-0.63	-0.08	-0.73	0.82	-0.35
May	0.29	0.33	0.96	0.86	0.61	0.19	0.93	0.62
June	0.26	0.30	0.94	0.82	0.86	0.61	0.98	0.90
July	-0.50	-0.20	0.75	0.29	0.68	0.53	0.94	0.81
August	-0.07	-1.05	-0.41	-1.09	0.07	0.17	0.88	0.53
September	-0.02	-0.01	-1.17	-2.25	-0.88	-1.74	0.46	-2.71
October	-0.68	-0.46	-0.23	-1.70	-7.78	-9.64	0.45	-2.59
November	-1.26	-3.92	0.73	-0.26	-2.96	-5.18	-1.20	-12.50
December	0.58	-0.82	0.56	0.72	0.68	-5.28	-1.66	-1.84
Annual	0.09	-0.05	0.66	0.20	0.58	-0.06	0.79	-0.18

this inflowing plume progresses through the reservoir, complete mixing is muted by densimetric resistance. If the plume's density is less than that of the reservoir, the plume will overflow reservoir water; the plume will underflow along the bottom or interflow at some intermediate depth when inflow density is greater than reservoir density. Turbulence at the boundaries continually erodes the density differences between the plume and surrounding water. The plume will tend to flow at a level equal to its density until it is either absorbed by the reservoir, reflected by a physical barrier or passed through the dam's outlet. Inflow temperatures and isopleth diagrams of water temperature for Lake Koocanusa reveal that underflow and interflow dominate throughout much of the year. The extent of the mixing zone and the eventual routing of

the inflow plume during reservoir filling, a time when influent loadings
of N and P were large, are depicted in Figure 9. After initial mixing,
the inflowing plume became either interflow, or initially underflow and
then interflow. Particulate P and clay-bound P were probably trans-
ported with the underflow and interflow currents and subsequently depo-
sited when the currents slowed.

The nutrient retention characteristics of Lake Koocanusa were simi-
lar to those reported for Kamloops Lake, British Columbia, by St. John
et al. (1976). Kamloops Lake retained 76% of its influent total P and
23% of its influent total N. Much of the total P loading, composed of
about 80% particulate P, was sedimented into the deep lake. The Thompson
River interflows through the lake and was presumed to have carried much
of the dissolved P and total N loadings through the lake.

Concentrations of N and P

The concentrations of N and P measured at the four reservoir sampl-
ing stations are listed in Appendix C. Mean yearly concentrations of
surface water total P, dissolved P and dissolved ortho-P ranged, respec-
tively, from 0.03 to 0.05 mg L^{-1}, 0.02 to 0.06 mg L^{-1}, and 0.01 to
0.02 mg L^{-1}. Mean yearly concentrations of bottom water total P, dis-
solved P and dissolved ortho-P ranged, respectively, from 0.05 to 0.09
mg L^{-1}, 0.04 to 0.08 mg L^{-1}, and 0.01 to 0.04 mg L^{-1}. As a gen-
eral rule, the bottom water concentrations of total P and dissolved P
and ortho-P measured on a particular date exceeded those measured at the
surface. Based on mean concentration, dissolved ortho-P represented 34%
of total P at the surface. At the bottom, dissolved ortho-P made up 47%
of total P.

Mean yearly concentrations of surface water total N and total
organic N ranged, respectively, from 0.21 to 0.33 mg L^{-1} and 0.09 to
0.38 mg L^{-1}, with mean total organic N being 39% of mean total N.
Mean yearly concentrations of bottom water total N and total organic N
ranged, respectively, from 0.22 to 0.46 mg L^{-1} and 0.09 to 0.34 mg L^{-1},
with mean total organic N being 31% of mean total N. In 1972, mean dis-
solved NH_3 ranged from 0.04 to 0.06 mg L^{-1} at the surface and 0.04
to 0.07 mg L^{-1} at the bottom. Total $NH_3 + NH_4^+$ was measured in
1973 through 1975 and the yearly mean concentration ranged from 0.03 to
0.15 mg L^{-1} at the surface and 0.03 to 0.14 mg L^{-1} at the bottom.

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b. 1973.

a. 1972.

24
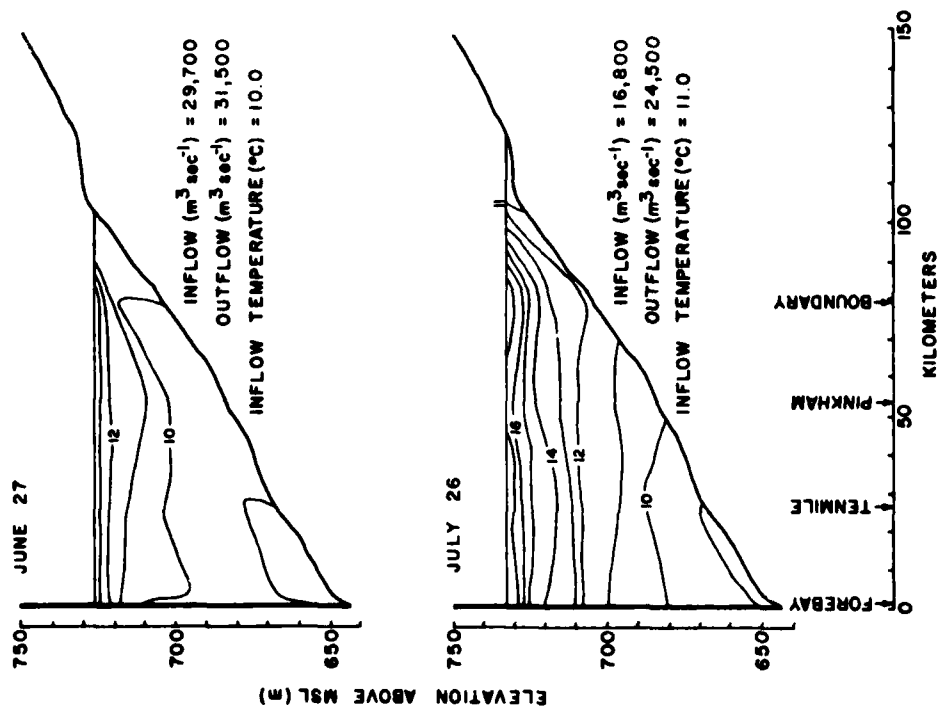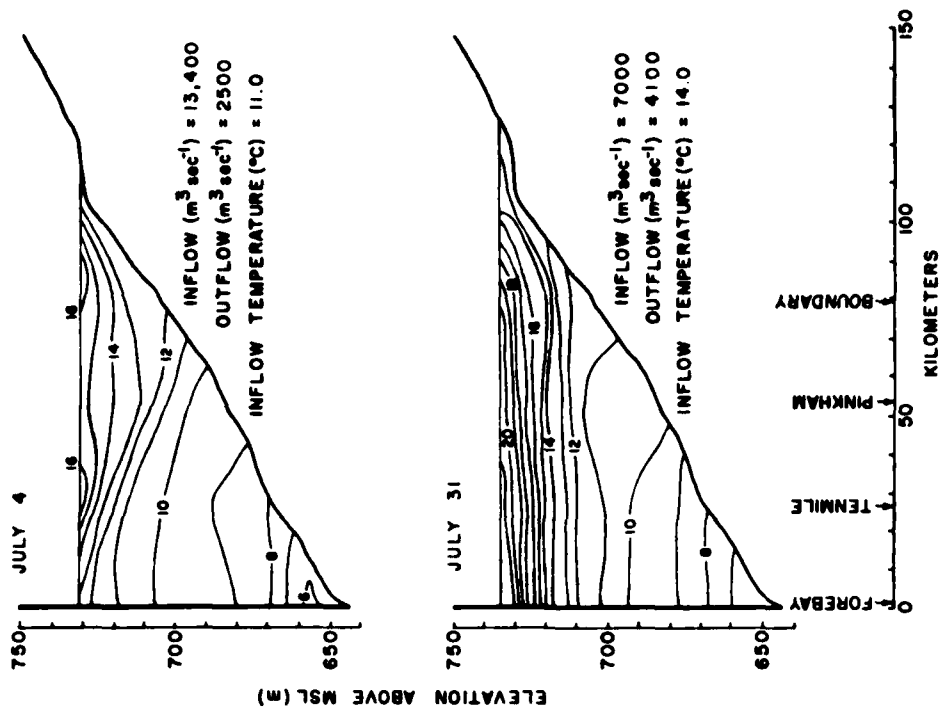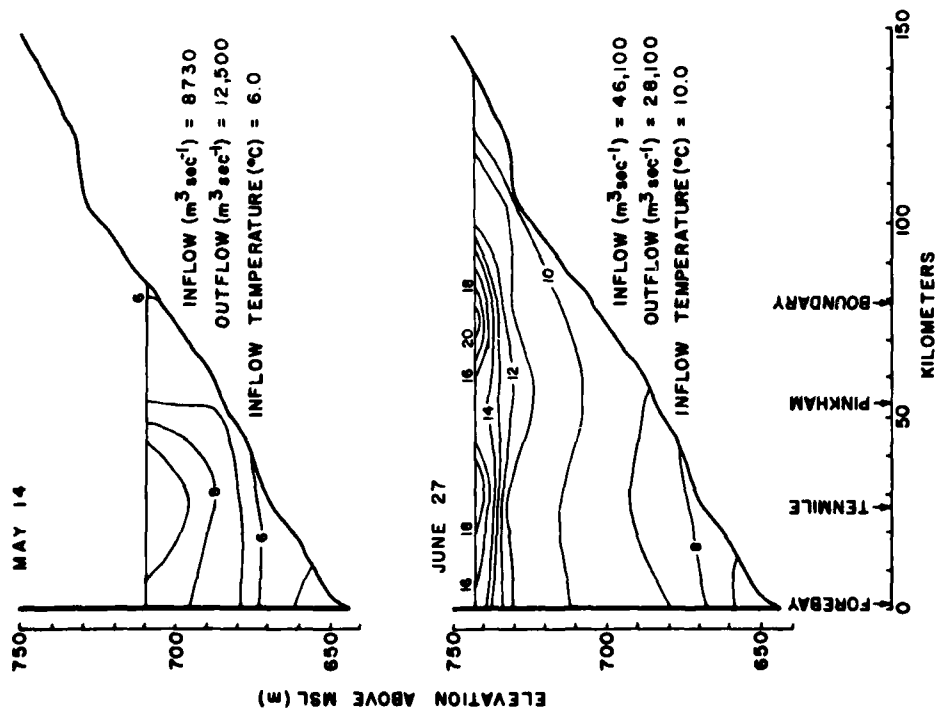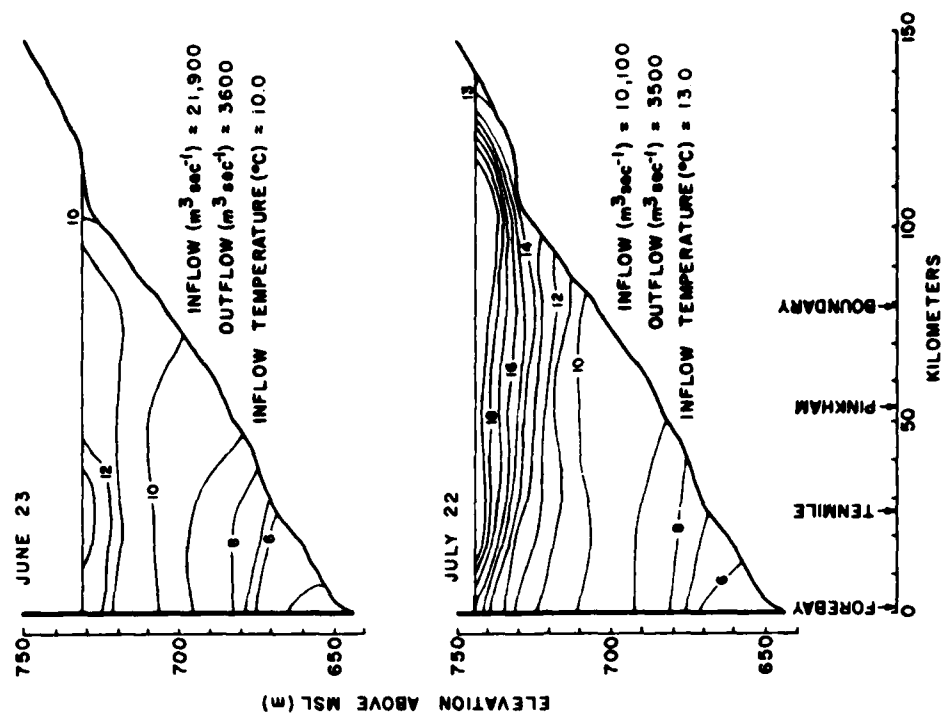
Figure 9. Thermal structure and inflow temperatures during filling of lake Koocanusa.

c. 1974.

d. 1975.

Mean yearly concentrations of dissolved nitrite (NO_2^-) plus nitrate (NO_3^-) ranged from 0.02 to 0.09 mg L^{-1} at the surface and 0.04 to 0.15 mg L^{-1} at the bottom. On the average, dissolved NO_2^- + NO_3^- was about 18 and 29% of total N at the surface and bottom respectively. NO_2^- represented, on the average, less than 5% of dissolved NO_2^- + NO_3^- values. In general, concentrations of total N and dissolved NO_2^- + NO_3^- measured on a particular date at the bottom exceeded those measured at the surface. Total organic N, dissolved NH_3, and total NH_3 + NH_4^+ showed less variation between bottom-water and surface-water samples on a particular date. During periods of water column circulation, differences between surface-water and bottom-water concentrations of N and P were muted, especially at the two upstream stations, Pinkham and Boundary.

Wetzel (1975) has listed some general criteria for ranking the potential trophic status of a lake based on N and P concentrations. The range of mean epilimnetic total P concentrations rank Lake Koocanusa as eutrophic, as do the lakewide concentrations of total P. Lakewide con-centrations of total N and mean epilimnetic organic N concentrations rank the reservoir as between oligotrophy and mesotrophy; whereas the mean epilimnetic concentrations of inorganic N rank the reservoir as ultraoligotrophic.

Sawyer (1947) concluded that for some southeastern Wisconsin lakes nuisance blooms of algae were likely if at the start of the growing season the lake contained 0.3 mg L^{-1} of inorganic N and 0.01 mg L^{-1} of soluble P. These criteria were frequently exceeded, to a large degree, by P concentrations in Lake Koocanusa, but rarely exceeded by inorganic N concentrations in the reservoir.

PRIMARY PRODUCTIVITY

Of the many methods used to categorize the trophic status of lakes and reservoirs, the C-14 light and dark bottle method for determining primary productivity is the most widely used. The method measures the rate of C fixation, in effect integrating the environmental influences controlling the production of organic matter.

Methodology

Primary productivities at the Forebay, Tenmile, Pinkham and Boundary stations were measured with the C-14 light and dark bottle method

described by Janzer et al. (1973). Water samples were placed in light
and dark BOD bottles and were inoculated with known amounts of radio-
active carbonate ($^{14}CO_3^{--}$). The BOD bottles were incubated in
situ within the euphotic zone for a measured time period, generally 3 to
4 hours. An aliquot of each sample was analyzed for its total content
of inorganic CO_3^{--}. Following incubation, the entire volume of a
BOD bottle was filtered through a membrane and the filter was washed
with 0.1 N hydrochloric acid to remove inorganic CO_3^{--}. Liquid
scintillation was used to measure the radioactivity assimilated into the
phytoplankton cells on the filters. Knowing the ratio of C-12 to C-14
in a BOD bottle prior to incubation and the amount of C-14 assimilated
by the phytoplankton during incubation permits calculation of the
quantity of C fixed as organic matter in the phytoplankton. This
calculated quantity was considered net primary productivity (Greeson et
al. 1977), expressed as milligrams of C fixed per cubic meter per hour
($mg\ C\ m^{-3}hr^{-1}$).

Estimates of primary productivity over a 24-hour day were made
following the methodology of Vollenweider (1965). Daily primary pro-
ductivities within the euphotic zone were integrated to determine areal
primary productivity, expressed as milligrams of C fixed per square
meter per day ($mg\ C\ m^{-2}day^{-1}$).

Seasonal variation

Areal primary productivities at the four stations over the 4 years
are shown in Figure 10 and statistically summarized in Table 11. Areal
productivities varied from less than 1 to 400 $mg\ C\ m^{-2}day^{-1}$. While
no one station consistently had the highest mean productivities, the
Pinkham station generally had the smallest. Tests to detect statis-
tically significant differences among stations and years were not
attempted because the sample time periods did not coincide. The Forebay
and Tenmile stations were sampled over a longer time because the Pinkham
and Boundary stations were inaccessible when the reservoir was drawn
down.

Annual primary productivity

Annual primary productivity for Lake Koocanusa and most other lakes
is difficult to accurately determine because the variations in primary
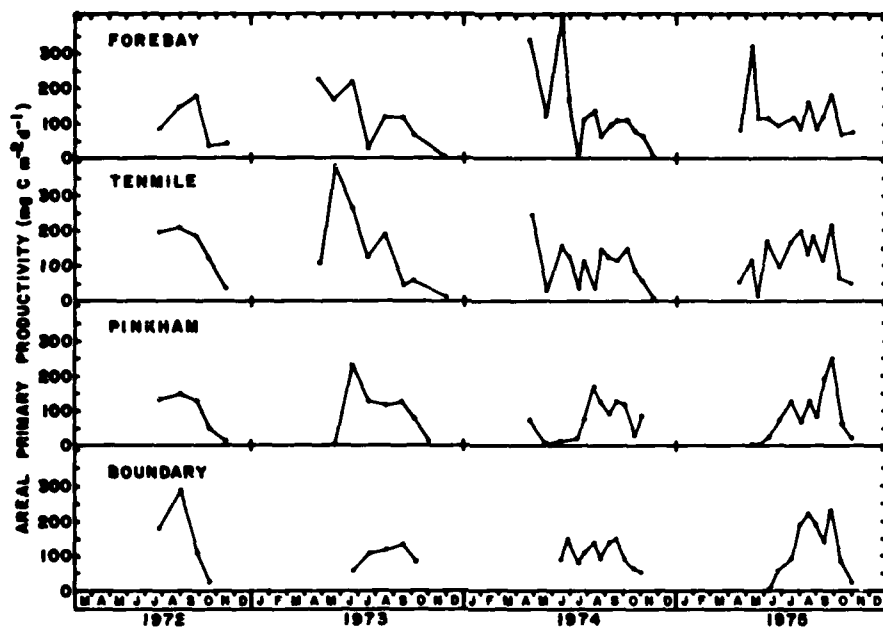
Figure 10. Areal primary productivity in Lake Koocanusa, 1972 through 1975.

Table 11. Statistical summary of areal primary productivity (mg C $m^{-2}day^{-1}$) in Lake Koocanusa, 1972-1975.

Station	Year	Mean	SD	Minimum	Maximum	n
Forebay	1972	100.2	62.2	40	180	5
	1973	120.5	83.4	4	230	8
	1974	130.4	111.5	3.2	400	14
	1975	125.8	66.9	70	320	13
	1972-1975	123.1	85.2	3.2	400	40
Tenmile	1972	152.6	70.7	43	210	5
	1973	151.5	126.9	12	390	8
	1974	105.9	65.1	5.1	250	14
	1975	125.2	63.6	16	220	13
	1972-1975	127.1	80.2	5.1	390	40
Pinkham	1972	92.7	63.4	1.4	150	5
	1973	100.4	78.7	0.5	230	7
	1974	80.6	51.9	2.1	170	12
	1975	87.3	76.4	1.7	250	12
	1972-1975	88.4	65.2	0.5	250	36
Boundary	1972	151.5	111.8	26	290	4
	1973	99.0	30.9	55	130	5
	1974	106.2	34.6	52	150	11
	1975	123.4	82.5	0.39	230	10
	1972-1975	116.8	65.0	0.39	290	30

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Table 12. Annual and mean daily areal primary productivity in Lake Koocanusa, 1972-1975.

Year	Annual primary productivity (g C m^{-2} yr^{-1})	Mean daily primary productivity (mg C m^{-2} day^{-1})
1972*	27.1	95.1
1973	38.5	105.5
1974	25.5	69.3
1975	24.4	66.8
1972-1975	28.8 (mean)	84.2 (mean)

*March 21 to December 31.

productivity has not been sufficiently quantified. In addition, many of the annual estimates found in the literature are based only on the primary productivity of phytoplankton, neglecting the annual contributions of littoral and benthic primary producers. However, in large and deep water bodies, the bulk of annual primary productivity is generally by phytoplankton (Wetzel 1975, Likens 1975) and this is likely the case in Lake Koocanusa.

The trophic status of lakes and reservoirs has been classified according to mean daily productivity (mg C $m^{-2}day^{-1}$) as follows: oligotrophic, 50 to 300; mesotrophic, 250 to 1,000; and eutrophic, greater than 1,000 (Wetzel 1975). Mean daily primary productivity may be calculated by dividing annual primary productivity by 365. To compare Lake Koocanusa with other lakes where primary productivity has been quantified, annual and mean daily primary productivities were calculated according to Vollenweider (1975). The results shown in Table 12 establish Lake Koocanusa as oligotrophic. Goldman (1977) considered Lake Tahoe to be ultraoligotrophic, with an average annual primary productivity of 55 g C $m^{-2}yr^{-1}$ over a period of 6 years. Of the Laurentian Great Lakes, Lake Superior has an annual primary productivity of 40 to 50 g C $m^{-2}yr^{-1}$ and is considered the least productive; Lake Erie is the most productive with an annual primary productivity of 240 to 250 g C $m^{-2}yr^{-1}$ (Vollenweider et al. 1974).

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Although the trophic characteristics of lakes Tahoe, Superior and
Erie are well known, it is not particularly enlightening to compare them
to Lake Koocanusa because they have longer retention times than Lake
Koocanusa. Kamloops Lake, British Columbia, is more like Lake Koocan-
usa. Lakes Koocanusa and Kamloops are long, narrow and deep, they have
short and highly variable retention times, they receive large volumes of
stratified interflow or underflow, and they receive large influent load-
ings of P. The annual and mean daily primary productivities determined
for the 3.7 km^3 Kamloops Lake were 32 g C $m^{-2}yr^{-1}$ and 88 mg C
$m^{-2}day^{-1}$ (St. John et al. 1976). Annual and mean daily primary
productivities in Lake Koocanusa were 28.8 g C $m^{-2}yr^{-1}$ and 84.2 mg C
$m^{-2}day^{-1}$ (Table 12).

In situ primary productivity

Multiple regression analysis

One goal in the analysis of an aquatic ecosystem might be the devel-
opment of a mathematical model capable of simulating the functional
behavior of the ecosystem. Such a model would require quantification of
the functional relationships among numerous variables, a prerequisite
not yet adequately achieved for an aquatic ecosystem such as Lake
Koocanusa. A viable alternative to a simulation model is a predictive
model developed by multiple regression analysis. Multiple regression
models may not be functionally realistic in total but they can ade-
quately reproduce the behavior of response and predictor variables and
provide insight into some relationships among variables.

A subset of variables sampled at Lake Koocanusa was analyzed by
multiple regression to determine those variables most capable of pre-
dicting areal primary productivity. The a priori selection of the 20
predictor variables (Table 13) was largely based on established causal
relationships between each variable and primary productivity. The data
base for the regression analysis was pooled observations taken at the
four reservoir stations within the United States. The periods June

Table 13. Statistical summary of response and predictor variables in multiple regression analysis of primary productivity in Lake Koocanusa.

Variables	Units	Mean[f]	SD
Primary productivity, areal	mg C $m^{-2}day^{-1}$	109.34	67.99
Euphotic chlorophyll 'a', areal[a,b,d]	mg m^{-2}	9.29	8.01
Euphotic chlorophyll 'a', volumetric[a,b,d]	mg m^{-3}	1.58	1.75
Euphotic total organic C[a,b]	mg L^{-1}	2.96	1.10
Euphotic total P as P[a,c]	mg L^{-1}	0.04	0.03
Euphotic dissolved ortho-P as P[a,c]	mg L^{-1}	0.02	0.02
Euphotic total organic N plus NH_3 + NH_4^+ as N[a,c]	mg L^{-1}	0.27	0.55
Euphotic total NH_3 + NH_4^+ as N[a,c]	mg L^{-1}	0.08	0.18
Euphotic dissolved NO_3^- as N[a,c]	mg L^{-1}	0.03	0.04
Euphotic CO_2 [a,c]	mg L^{-1}	1.08	0.40
Euphotic dissolved Si as SiO_2 [a,c]	mg L^{-1}	4.64	1.00
Euphotic total dissolved solids[a,c]	mg L^{-1}	118.70	20.68
Surface illumination[e]	ft-candles	2,733.72	1,836.89
Euphotic extinction coefficient[a]	--	2.77	3.55
Euphotic temperature[a]	C	14.33	3.79
Stability of primary thermocline	g cm^{-2}	8.42	8.87
Stability of secondary thermocline	g cm^{-2}	6.73	27.02
Epilimnion-euphotic ratio	--	4.83	7.15
Retention time	days	260.42	200.16
Flushing time	days	322.11	267.47
Areal loading	m yr^{-1}	136.99	157.52

[a]Depth weighted average of euphotic zone measurements.
[b]Analysis per Goerlitz and Brown (1971).
[c]Analysis per Brown et al. (1970).
[d]Not corrected for phaeopigments.
[e]Time weighted average of measurements during C-14 incubations.
[f]93 observations per variable.

through November 1974 and April through October 1975 were analyzed using the 93 observations taken on each of the response and predictor variables.

Three of the variables, epilimnion-euphotic ratio, stability of primary thermocline, and stability of secondary thermocline were indices of thermal structure. Epilimnion-euphotic ratios were determined as epilimnion depth divided by euphotic zone depth. Stabilities of the primary and secondary thermoclines represent the vertical stability gradients respectively associated with the stratum of maximum resistance to mixing and the stratum next most resistant to mixing that overlaid the primary thermocline.

Areal loading was calculated using the following equation:

$$AL = \frac{I}{A}$$

where AL is areal loading in m yr^{-1}, I is inflow in $m^3 yr^{-1}$, and A is surface area in m^2. The areal loading variable was included because of its correlation with the P retention capacity of low productivity lakes reported by Larsen and Mercier (1976).

A set of regression models was calculated that contained the number (n = 1 to 20) of predictor variables that best described the variation in areal primary productivity. The Statistical Analysis System (Barr et al. 1976) regression procedure is a modification of stepwise multiple regression and uses maximal improvement of the squared multiple correlation coefficient (R^2) as the criterion for chosing the model with the largest R^2. The prediction model chosen was the one with the largest R^2 and in which all the included variables were significant ($p < 0.05$).

The best model for predicting areal primary productivity used the following six predictor variables: euphotic extinction coefficient, areal loading, euphotic total dissolved solids, stability of primary thermocline, surface illumination and flushing time (Table 14). This model accounted for 50.0% of the variation in areal primary productivity and was significant ($p < 0.001$). The best 20-variable model for prediction of areal primary productivity accounted for 58.0% of the variation, but the only significant ($p < 0.05$) variables were surface illumination, euphotic total P, euphotic total dissolved solids, stability of primary thermocline, and areal loading.

Where the variables in a multiple regression model have been measured in different units, the relative effect of each predictor variable on the response variable will be revealed by the standardized partial regression coefficients (Kim and Kohout 1975). The standardized partial regression coefficients (Table 14) showed that the relative influence of the six predictor variables in the best model describing areal primary productivity was ordered from greatest to least as follows: euphotic extinction coefficient, areal loading, euphotic total dissolved solids, stability of primary thermocline, surface illumination, and flushing time. Areal primary productivity was inversely related to euphotic

Table 14. Multiple regression model for predicting areal primary productivity in Lake Koocanusa.

Model

$$Y = -62.12 - 12.95X_1 + 0.17X_2 + 1.04X_3 + 2.12X_4 + 0.0.X_5 + 0.05X_6$$

where Y = areal primary productivity $\quad\quad$ X_4 = stability of primary thermocline

X_1 = euphotic extinction coefficient $\quad\quad$ X_5 = surface illumination

X_2 = areal loading $\quad\quad$ X_6 = flushing time

X_3 = euphotic total dissolved solids

Multiple R = 0.707 $\quad\quad$ Multiple R^2 = 0.500 $\quad\quad$ Standard error = 49.705

Analysis of variance

Source	df	Sum of squares	Mean square	F
Total	92	425241.073	--	--
Regression	4	212774.385	35462.398	14.354**
Residual	88	212466.688	2470.688	--

Predictor variable summary

Variable	Partial regression coefficient	Standardized partial regression coefficient	Standard error, partial regression coefficient	F
Euphotic extinction coefficient	-12.95	-0.677	2.022	41.009**
Areal loading	0.17	0.391	0.050	11.761**
Euphotic total dissolved solids	1.04	0.315	0.287	13.002**
Stability of primary thermocline	2.12	0.276	0.662	10.200+
Surface illumination	0.01	0.265	0.003	10.299+
Flushing time	0.05	0.208	0.021	5.975*

*Significant at $p < 0.025$.
+Significant at $p < 0.005$.
**Significant at $p < 0.001$.

extinction coefficient and directly related to the other five variables. Plots of standardized residuals and the standardized predicted values of the response variable revealed no gross departures from the assumptions of regression analysis as discussed by Draper and Smith (1966) and Kim and Kohout (1975).

Variability was evident in plots of the response and six predictor variables with time (Fig. 11) and in scatterplots of the response versus predictor variables. Although most of the scatterplots indicated non-linearity, no appropriate transformations were evident. Because of the variability and nonlinearity, the 20-variable regression model explained only 58.0% of the variation in areal primary productivity. The variability could have possibly been reduced by subdivision of the multiple
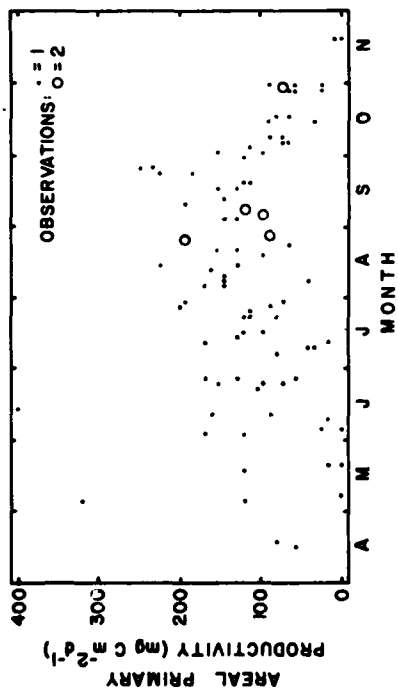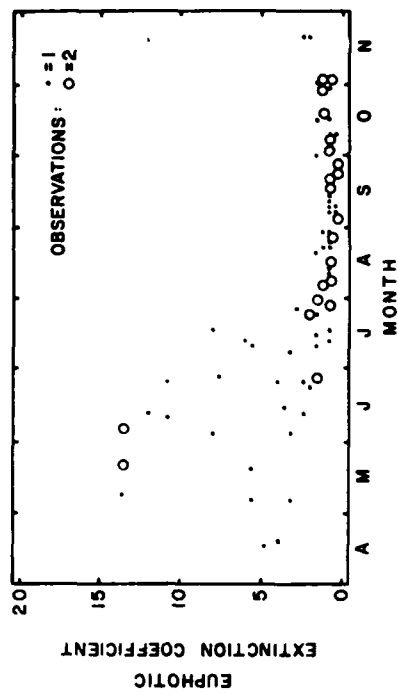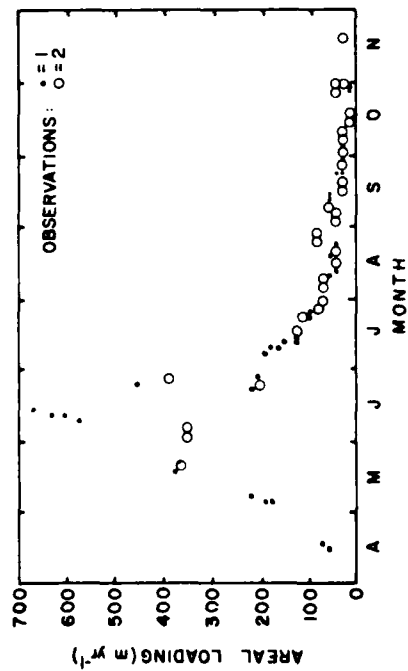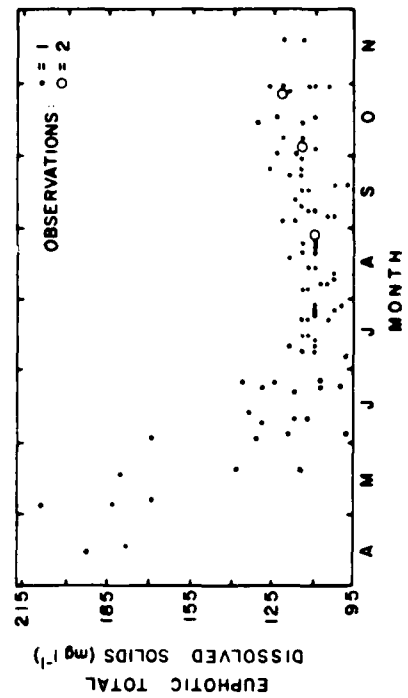
b. Euphotic extinction.

d. Euphotic total dissolved solids.

a. Areal primary productivity.

c. Areal loading.

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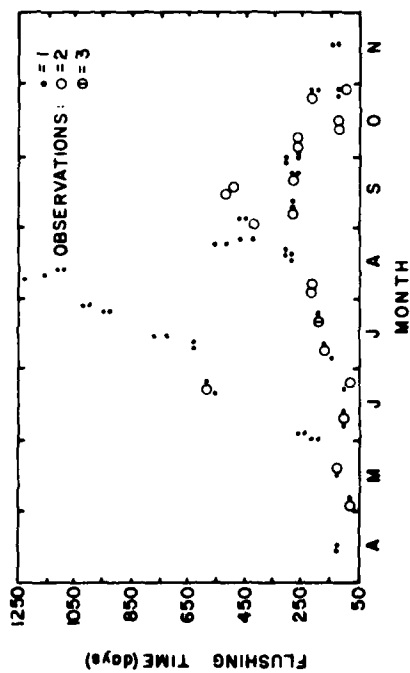
f. Surface illumination.

e. Stability of primary thermocline.
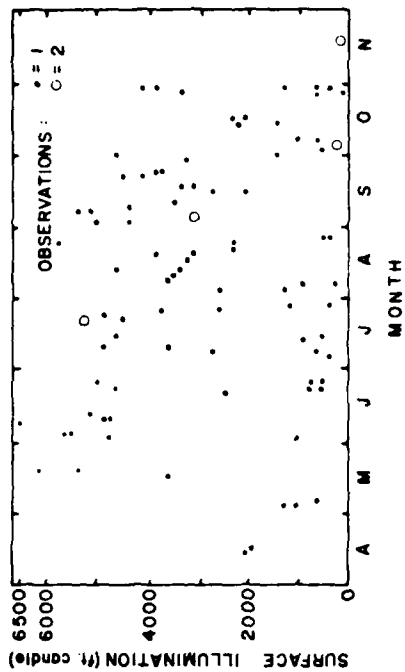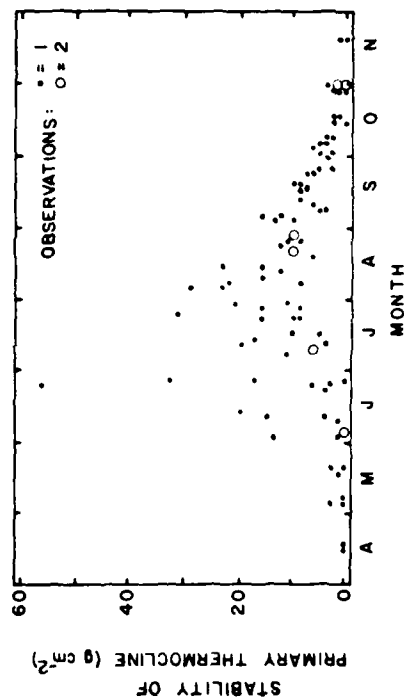
g. Flushing time.

Figure 11. Temporal changes in variables used in regression model for predicting primary productivity in lake Koocanusa, 1974 through 1975.

regression analysis by year, by station, or by station and year; however, sample sizes for each analysis would have been substantially reduced. The primary intent of the multiple regression analysis was to determine those variables most influential to primary productivity on a reservoir-wide basis.

Areal primary productivity (Fig. 11a) was inversely related to euphotic extinction coefficient (Fig. 11b). The large extinction coefficients in April through May were associated with a wide range of production rates; the small post-July extinction coefficients occurred with production rates closer to the mean rate of about 110 mg C $m^{-2}day^{-1}$. Areal loading (Fig. 11c) and euphotic total dissolved solids (Fig. 11d) were directly related to areal productivity due to the coincidence of their large springtime values and low wintertime values. The wide variations in surface illumination (Fig. 11f) apparently obscured its direct relationship with areal primary productivity. Stability of primary thermocline (Fig. 11e) and flushing time (Fig. 11g) varied together and were directly related to areal primary productivity.

Of the six predictor variables in the best regression model, all but euphotic total dissolved solids represented physical aspects of Lake Koocanusa's aquatic environment. Similarly, the first order correlation coefficients between the response and predictor variables (Table 15) revealed that the only variables with significant ($p < 0.05$) correlations greater than 0.30 were stability of primary thermocline, epilimnion-euphotic ratio, and euphotic extinction coefficient. Again, these three variables represented physical aspects of the reservoir's limnology. Areal loading and flushing time represented hydrologic aspects of Lake Koocanusa. Stability of primary thermocline and epilimnion-euphotic ratio were indices of water column circulation. Euphotic extinction coefficient and surface illumination were variables representative of the reservoir's photic environment. The variation in euphotic total dissolved solids was closely tied to reservoir hydrology because the large inflow of snowmelt runoff in the spring rapidly diluted the concentration of total dissolved solids. Some variables with statistically significant first order correlations did not appear in the best multiple regression model. The relative magnitude of a partial correlation coefficient for a predictor variable may differ from its first order correlation with the same response variable because the first order

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Table 15. Correlations between predictor variables and areal primary productivity in Lake Koocanusa, 1974 and 1975.

Predictor variables	Correlation, coefficient[++]
Euphotic chlorophyll 'a', areal	0.143
Euphotic chlorophyll 'a', volumetric	-0.011
Euphotic total organic C	-0.258[+]
Euphotic total P as P	-0.224*
Euphotic dissolved ortho-P as P	0.107
Euphotic total organic N plus $NH_3 + NH_4^+$ as N	-0.171
Euphotic total $NH_3 + NH_4^+$ as N	-0.186*
Euphotic dissolved NO_3^- as N	-0.268[+]
Euphotic CO_2	-0.258[+]
Euphotic dissolved Si as SiO_2	0.031
Euphotic total dissolved solids	0.059
Surface illumination	0.237*
Euphotic extinction coefficient	-0.347**
Euphotic temperature	0.291[+]
Primary thermocline stability	0.364**
Secondary thermocline stability	0.005
Epilimnion-euphotic ratio	-0.456**
Retention time	-0.082
Flushing time	0.227[+]
Areal loading	0.093

*Significant at $0.01 < p < 0.05$.

+Significant at $0.001 < p < 0.01$.

**Significant at $p < 0.001$.

++93 observations per variable.

correlation may be confounded by correlation with other predictor variables (Kim and Kohout 1975).

The multiple regression analysis and correlation coefficients revealed some relationships between the environmental variables and areal primary productivity but the strengths of these relationships were obscured by the variability and nonlinearity inherent in the variables. Because the multiple regression analysis was inconclusive, the areal

primary productivities measured in situ were evaluated in conjunction
with those environmental variables likely to have controlled primary
productivity in Lake Koocanusa.

Environmental control of in situ primary productivity

The environmental variables with a significant effect upon the pro-
ductivity and seasonal dynamics of phytoplankton were categorized by
Hutchinson (1967) as follows: 1) partially independent physical factors
composed of temperature, light and turbulence, 2) interdependent bio-
chemical factors composed of inorganic and organic nutrients and
accessory organic compounds, and 3) the biological factors of predation,
parasitism and competition. No one variable will fully account for
variations in primary productivity because the aquatic environment is a
dynamic medium in which phytoplankton respond within tolerance ranges to
the simultaneous interaction of a large array of environmental variables.

Nutrients. Phytoplankton require various inorganic and organic
nutrients in macro and micro quantities for their growth. An essential
nutrient may limit growth if not in sufficient supply. Based on the
ratio of a freshwater plant's demand for a nutrient to the supply of
that nutrient in the surrounding water, growth is most likely to be
nutritionally limited by P, N, C and Si (Vallentyne 1974).

Phytoplankton growth may be limited by a deficiency of inorganic C,
but only in water bodies of low alkalinity, extreme hardness, or hyper-
eutrophication (Wetzel 1975). Water in Lake Koocanusa meets none of
these conditions. The total hardness of water released through Libby Dam
in 1972 through 1975 was moderately hard to hard, according to the
criteria of Hem (1970). The mean epilimnetic total alkalinity in the
reservoir for 1972 through 1975 was approximately 90 mg L^{-1} $CaCO_3$,
well above the American Public Health Association's (1976) low alka-
linity designation of less than 20 mg L^{-1} $CaCO_3$. The suppression of
diatom growth associated with Si concentrations less than 0.5 mg L^{-1}
(Wetzel 1975) was unlikely in Lake Koocanusa because the lowest reported
concentrations were greater than 3.0 mg L^{-1}.

Eutrophication research has repeatedly demonstrated that shortages
of P and N most often limit aquatic plant growth (Rast and Lee 1978).
The forms of N and P in fresh water which are readily available to
phytoplankton are soluble ortho-P, NO_3^- and NH_4^+. Atmospheric

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N may be fixed by algae when other N sources have been depleted; however, this ability is restricted to several of the blue-green algae, such as Aphanizomenon flos-aquae (Fogg 1974). The algal blooms in Lake Koocanusa in the autumn of 1974 and 1975 were predominantly A. flos-aquae (Bush and Bonde 1977).

When concentrations of 0.2 to 0.3 mg L^{-1} inorganic N and 0.01 to 0.02 mg L^{-1} inorganic P are present at the start of the growing season, nuisance algal blooms are likely (Mackenthun 1965). The epilimnetic concentrations of inorganic N ($NO_2^- + NO_3^- + NH_4^+$ as N) and soluble ortho-P (PO_4^{---} as P) measured in Lake Koocanusa are shown in Figure 12. The soluble ortho-P concentrations in the reservoir often exceeded 0.02 mg L^{-1} but inorganic N concentrations rarely exceeded 0.2 mg L^{-1}. During the late summer and autumn, the two nutrients occasionally declined to less than detectable concentrations.

Low nutrient concentrations do not necessarily imply nutrient limitation of phytoplankton because in situ concentrations only reflect the instantaneous balance between the supply and consumption of a nutrient (Fogg 1975). The P data from the reservoir were inadequate for assessing nutrient limitation of phytoplankton because concentrations were only reported to 0.01 mg L^{-1}; phytoplankton growth has been reported at inorganic P concentrations below this figure (Hutchinson 1967).

The N and P data taken concurrently with areal productivity did not appear to account for the seasonal variations in productivity in Lake Koocanusa. Declines in productivity were often associated with increased nutrient concentrations; in other instances, decreased nutrient concentrations were coupled with increases in productivity. Such a lack of correlation supports the contention of Schindler and Fee (1975) that in situ nutrient concentrations provide a poor means of assessing variations in primary productivity.

Temperature. Phytoplankton physiology is temperature-dependent, but the influence on primary productivity of temperatures normally encountered by phytoplankton has often been obscure (Taylor 1972). This is due in part to the interrelated effects of temperatures, light and nutrients on the metabolism and photosynthesis of phytoplankton. In addition, consideration of temperature has often been unnecessary in
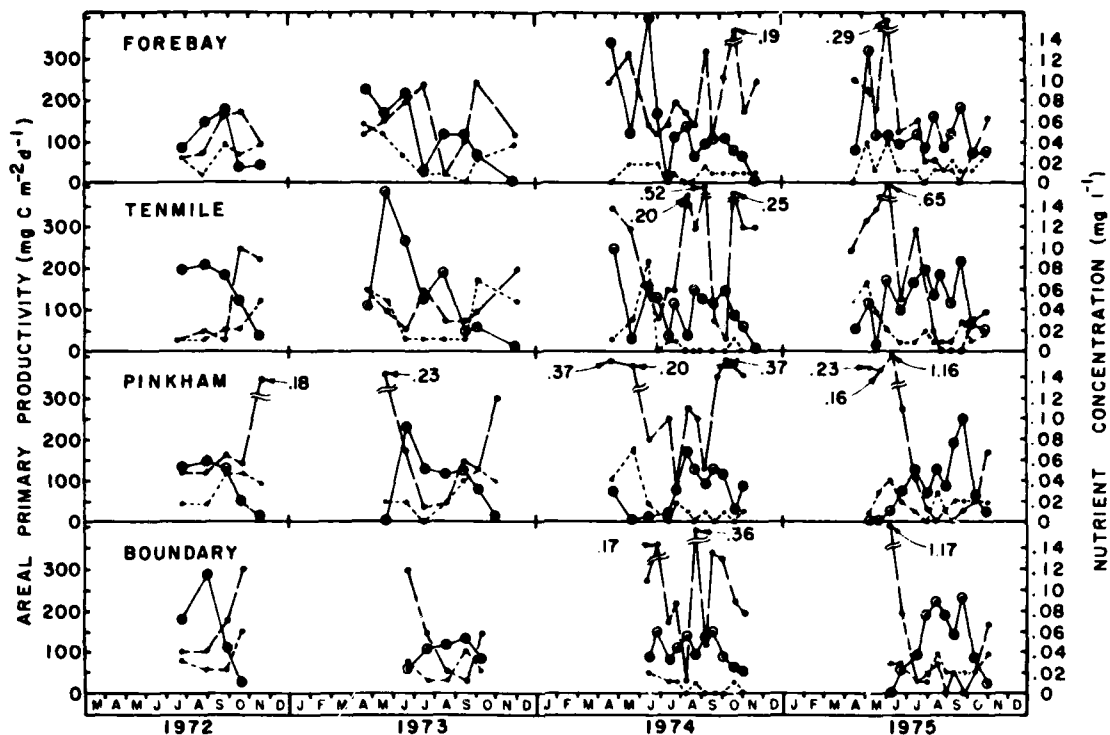
Figure 12. Areal primary productivity (—⊖—), epilimnetic inorganic N (— —•), and epilimnetic soluble othrophosphate (—•—) in Lake Koocanusa, 1972 through 1975.

mathematical models of pelagic primary productivity limited by light or nutrients (Stengel and Soeder 1975).

No clear relationship was found between the seasonal variations of near-surface water temperatures and areal primary productivity in Lake Koocanusa. Reservoir water temperatures, measured at the 3.1-m depth, typically increased steadily from an April low of less than $4°$ C to an August high of between $18°$ and $20°$ C and then steadily declined to minimum winter temperatures. This pattern was quite different from that of areal primary productivity in the reservoir (Fig. 12).

Turbulence. The turbulent transport of biotic and abiotic components is a major environmental controller of lacustrine primary productivity. A phytoplankton cell's position in the water column largely determines its ability to photosynthesize in excess of respiratory requirements and, hence, achieve positive net primary productivity. Photosynthesis and respiration are approximately equal at the lower boundary of the

euphotic zone, the depth at which light intensity is 1% of that incident
upon the surface. Talling (1962) reported that phytoplankton photo-
synthesis was generally insignificant at less than 1% light intensity.
Therefore, a phytoplankter transported below the euphotic zone should
achieve negative net primary productivity.

Most planktonic organisms have a density slightly greater than that
of water and will sink in calm water (Hutchinson 1967); some have modi-
fied sinking rates or can even float with adaptations such as production
of mucilaginous sheaths, gas vacuoles, fat accumulation, or shape alter-
ations to attain a more favorable surface-to-volume ratio. Except for
the buoyancy regulation achieved with gas vacuoles or the motility of
flagellates, such modifications only retard sinking; most phytoplankton
remain in the euphotic zone because of turbulence. Sinking is not with-
out its benefits in that it augments nutrient uptake by maintaining a
concentration gradient at the cell's surface.

Under well-stratified conditions, the thermocline is the lower
boundary of turbulent mixing, and circulation will therefore be restric-
ted to the epilimnion. When stratification is weak or absent, turbulent
mixing may penetrate deep into the water column. In the case where
mixing extends below the euphotic zone, phytoplankton will be circulat-
ing throughout the epilimnion, thereby spending part of their time in
light conditions inadequate for photosynthesis.

The potential for deep circulation of phytoplankton in Lake Koocan-
usa was assessed with data on the relative depths of the epilimnion and
euphotic zones, the previously defined epilimnion-euphotic ratio. Of
the 145 epilimnion-euphotic ratios computed, only 23 were equal to or
less than 1:1 (the case in which the epilimnion was contained within the
euphotic zone). The epilimnion-euphotic ratios and relative stability
data attest to the weak thermal structure of Lake Koocanusa and lend
support to the hypothesis that phytoplankton were frequently transported
below the euphotic zone.

Light. Light and primary productivity are closely related in that
photosynthesis is a biochemical oxidation-reduction reaction driven by
light energy. The light energy that stimulates photosynthesis consti-
tutes only a small portion of the range of wavelengths within the solar

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spectrum. Photosynthetic pigments respond to light over a range of
wavelengths from 390 to 710 nm (Vollenweider 1974). The photosynthetic
rate increases with increasing light intensity until a maximal photo-
synthetic rate is reached at light saturation. Further increases in
light intensity produce little change in the photosynthetic rate until
light intensities increase to the point where photo-oxidation destroys
enzymes and causes photosynthesis to decline.

Light-photosynthesis curves vary among algal species mostly because
of two ways of adapting to light intensity (Soeder and Stengel 1975).
In one, the photosynthetic rate is relatively constant but concentrations
of photosynthetic pigments change in response to light intensity. In
the other, pigment concentrations remain unaltered but the rates of
photosynthetic processes vary. The shapes of light-photosynthesis
curves and the levels of light-saturated photosynthesis are temperature
dependent, thus the effects of light and temperature on photosynthesis
are inseparable (Soeder and Stengel 1975). Although not within the
photosynthetically active range, the infrared portion of incident solar
radiation is important in determining the temperatures experienced by
phytoplankton.

Depth profiles of primary productivity (Appendix D) were evaluated
to determine the effects of light on areal primary productivity measured
in Lake Koocanusa. The shapes of such profiles are primarily determined
by the photosynthesis-light relationship, the light attenuation charac-
teristics of the water column, and vertical distribution and abundance
of phytoplankton (Talling 1975). In that water column circulation helps
determine an algal cell's exposure to light, the productivity profiles
were evaluated in conjuction with the previously discussed eplimnion-
euphotic ratios and relative stabilities.

Weak stability and circulation below the euphotic zone frequently
occurred but failed to account for variations in areal primary produc-
tivity. Production was usually higher in the spring and autumn, periods
of weak stability and deep circulation. A diatom-produced springtime
high in primary productivity is common in temperate lakes and is caused
primarily by increased light (Lund 1965, Wetzel 1975), although an ade-
quate nutrient supply is also requisite (Hutchinson 1967). As revealed
by a computer simulation of phytoplankton population dynamics, diatoms

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needed rapid division rates, made possible by adequate nutrients, and turbulence to achieve net population growth in the spring (Lehman et al. 1975). Increased primary productivities during autumn circulation have been linked to a resuspension of nutrients (Fogg 1975); however, the trends in N and P concentrations in Lake Koocanusa do not support this hypothesis. In the autumn of 1974 and 1975, the highest primary productivities were found on days when observers noted blooms of the N-fixing blue-green algae, Aphanizomenon flos-aquae. The combination of an epilimnion-euphotic ratio near 1:1, a relative stability greater than 100%, and full sunlight occasionally yielded the high areal primary productivity expected under such idealized conditions; however, this was the exception to the general trend, as shown in Figure 10.

Euphotic zone depth, determined by extinction coefficients and incident surface light intensity, accounted for much of the variation in areal primary productivity measured in Lake Koocanusa. As highly turbid snowmelt runoff filled the reservoir, euphotic zone depths were substantially reduced, in some instances to less than 1 m (Fig. D1b, D2b, and D2d). Areal primary productivities at the Boundary and Pinkham stations were quite low until their euphotic zones deepened. Euphotic zone depths were not as severely reduced at the Tenmile and Forebay stations, hence areal primary productivities were not as severely reduced. Soltero and Wright (1975) reported similar trends in the newly impounded Bighorn Lake in Montana. These authors attributed low areal primary productivities in the upper end of the reservoir to light limitation caused by turbid inflow. Areal primary productivities increased as the euphotic zone deepened.

Although much of the turbidity in Lake Koocanusa was due to suspended sediment, the potential impact of biogenic turbidity should be addressed. Inverse correlations between light penetration and planktonic population density have been reported (Fogg 1975), but Talling (1960) concluded that only rarely does self-shading by high population density severely reduce light intensity within the water column. Phytoplankton population densities were probably low in Lake Koocanusa, considering the mean chlorophyll 'a' concentration of 1.58 mg m^{-3} (Table 13). Wetzel (1975) classified as oligotrophic those water bodies with a chlorophyll 'a' concentration between 0.3 and 3 mg m^{-3}.

Many of the low primary productivities occurred with the low surface light intensities of late autumn, winter and overcast days. Insolation recorded at Libby Dam showed that sunny days in July and late October received 677 and 266 langleys respectively. A cloudy day in July received only 268 langleys. High light intensities frequently caused photoinhibition of phytoplankton incubated in the upper euphotic zone and a consequent reduction of areal primary productivity. Circulating phytoplankton may experience rapid shifts in light intensity to which they must adapt their photosynthetic processes. The rapidity of this adaptation and the ability of the phytoplankton to recover from photo-inhibition varies among species (Lund 1965). Talling (1962) concluded that the overall impact of inhibition of photosynthesis at the water surface is uncertain for phytoplankton that undergo deep circulation. For example, the second highest rate of areal primary production was measured at the Tenmile station in May 1973, in a strongly illuminated, 1-m deep euphotic zone. The impact of photoinhibition on the primary productivity in Lake Koocanusa was considered negligible.

Parasitism, predation and competition. The impacts on areal primary productivity of parasitism, predation and competition are conjectural because no specific data on these impacts were collected from Lake Koocanusa. The occurrence of bacterial, viral and fungal parasitism of phytoplankton has been established but effects on phytoplankton popula-tions are poorly understood (Wetzel 1975). Significant infestations are more likely in eutrophic water bodies (Hutchinson 1967).

Studies of zooplankton predation on phytoplankton have yielded ambiguous results (Wetzel 1975). It is difficult to isolate grazing as a significant influence on phytoplankton populations because of the numerous predator-prey interactions involved (Hutchinson 1967). In a study of Dworshak Reservoir in northern Idaho, Skille (1977) partitioned the phytoplanktonic production lost from the epilimnion into losses due to sinking, recycling within the epilimnion and zooplankton grazing. Skille determined that only 9.5% of the mean loss of phytoplankton pro-duction through the summer and fall could be attributed to zooplankton grazing.

Competition among species is involved in the seasonal succession of

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phytoplankton populations. Seasonal variations in primary productivity
are also affected by competition because many of the environmental vari-
ables for which phytoplankton compete have major influences on phyto-
plankton physiology. The dynamic nature of these environmental variables
denies a long term competitive advantage to any one species and thereby
prevents establishment of a unispecific equilibrium. Hutchinson (1967)
alluded to an apparent case of competition in which an N-fixing blue-
green algae, Anabaena circinalis, became dominant over the diatom
Fragilaria crotonesis when inorganic N had become severely depleted.
The appearance of Aphanizomenon flos-aquae in Lake Koocanusa is a
similar situation. The presence of warm water, low concentrations of
inorganic N and the buoyancy regulation of this blue-green alga may have
allowed it a temporary competitive advantage over other algae species
present.

The interaction of physical, chemical and biological variables pre-
vented any one variable from dominating primary productivity, but much
of the variability of in situ areal primary productivity in Lake Koocan-
usa was attributable to the controlling influence of the intensity of
light. The significant variables derived by the multiple regression
analysis included euphotic extinction coefficient, surface illumination,
stability of the primary thermocline, and epilimnion-euphotic ratio;
these have been shown to be either directly or indirectly associated
with light intensities available to phytoplankton. The reservoir's weak
thermal structure and consequent circulation offer strong intuitive evi-
dence of the suppression of primary productivity. The in situ profiles,
representative of the final outcome of the interplay of environmental
variables with phytoplankton productivity, were not, however, explain-
able in terms of circulation of phytoplankton below the euphotic zone.

Factors responsible for oligotrophy in Lake Koocanusa

The productivity profiles provided a means for attributing the vari-
ations of in situ areal primary productivity to specific environmental
variables, but did not pinpoint the mechanisms responsible for the
oligotrophic nature of Lake Koocanusa. The reservoir's potential for
eutrophy, predicted from the large nutrient loadings and manifested by
the blooms of blue-green algae and high concentrations of epilimnetic P,

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prompts further analysis to elucidate those mechanisms which suppressed phytoplankton production and resulted in the oligotrophy of Lake Koocanusa.

Solar Radiation

Autochthonous and allochthonous sources of phytosynthetically fixed C provide the main energy sources driving lacustrine production. In addition to its role in photosynthesis, solar energy is the principal heat source for most water bodies. Some reservoirs with large inflows may, however, receive much of their thermal energy from influent streams (Wunderlich and Elder 1967). Absorption and distribution of heat determine a water body's thermal structure which, in turn, influences the physical, chemical and biological components of the aquatic environment.

Incident solar radiation is a function of latitude, altitude, season, time of day and local meteorological conditions. The seasonal variation in solar radiation at higher latitudes is a major control of the seasonal cycles of primary production (Golterman 1975). A multiple regression analysis of lakes and reservoirs distributed from the tropics to the arctic revealed that 57% of the variation in annual primary production could be accounted for by latitude alone (Brylinsky and Mann 1973). These results have been reinterpreted by Schindler (1978) who added nutrient loading variables to the original data base. Schindler reported a nonsignificant correlation between annual primary production and latitude, but he cautioned that his results may have been biased because nutrient loading data were primarily available for temperate lakes and reservoirs.

Expected solar radiation to the northwestern United States in December (Odum 1971) is only 20% of that expected in July. Winter solar radiation at Lake Koocanusa resulted in low light intensities as well as low water and air temperatures. The declining rates of primary production measured in autumn and early winter were more likely due to low light intensity than to low water temperatures. The minimum temperature required for diatom photosynthesis in excess of maintenance levels is about 5° C (Wetzel 1975). The earliest appearance of water temperatures lower than 5° C was mid-November at the Boundary station. Winter primary production may substantially add to annual primary production if algal species adapted to low light and temperature are able

to grow. No data were available to assess winter primary production in Lake Koocanusa, but its contribution was probably small in light of the nearly 70% reduction in reservoir surface area during winter drawdown.

Seasonally and meteorologically induced variations in incident solar radiation were major controllers of primary productivity in Lake Koocanusa. Also of major importance were extinction coefficients as determinants of light penetration into the reservoir, and thermal structure as a determinant of an algal cell's ability to receive light adequate for photosynthesis. The hydrodynamic behavior of the reservoir was a principal determinant of extinction coefficients and thermal structure.

Hydrodynamics

The weak thermal structure and preponderance of epilimnion-euphotic ratios greater than 1:1 imply that primary productivity in Lake Koocanusa was suppressed by circulation of phytoplankton below the euphotic zone. Suppression of lacustrine primary productivity by circulation of phytoplankton below the euphotic zone has been noted in general terms by Murphy (1962), Lund (1965), Hutchinson (1967), Fogg (1975) and Wetzel (1975). Stadelmann et al. (1974) reported that the spring increase in primary productivity at a near shore station in Lake Ontario occurred one month earlier than at an offshore station. The authors attributed the time lag and the lower productivity of the offshore station to that station's deep circulation; it became stratified one month later than did the near shore station. St. John et al. (1976) reasoned that the oligotrophic levels of primary productivity in Kamloops Lake, British Columbia, were caused by circulation of phytoplankton below the euphotic zone. Epilimnion depths in Kamloops Lake were 3 to 21 times greater than euphotic zone depths; such circulation was caused by the large volumes of the Thompson River flowing at intermediate depth through the lake (St. John et al. 1976).

The approach of St. John et al. (1976) was used to approximate the relative magnitude of suppression of primary productivity in Lake Koocanusa. St. John et al. (1976) theorized that in a perfectly mixed epilimnion, primary productivity would be reduced in direct proportion to the epilimnion-euphotic ratio because a phytoplankter would spend that proportion of its time below the euphotic zone. If the mean epilimnion-euphotic ratio of 4.83:1 (Table 13) is representative of the

ratio of suppression, it appears that areal primary productivity in Lake Koocanusa attained only 20.7% of its potential. An accurate ratio of suppression cannot be ascertained because the assumption of a perfectly mixed epilimnion was invalid. Transitory stratification in Lake Koocanusa resulted in a deep, weak thermocline often briefly overlain by secondary or multiple thermoclines.

Losses through outlet

Primary production in lakes and reservoirs may be suppressed by flushing of abiotic and biotic materials through the outflow. Flushing of living phytoplankton decreases phytoplankton populations (Dickman 1969), in addition to population losses due to grazing, sinking and cell mortality caused by parasites or the physiological extremes listed by Jassby and Goldman (1974). Nutrients will also be flushed and in some instances this may keep potentially eutrophic situations in check. Dillon (1975) noted that P removal due to high flushing rates may counteract high influent loadings of P. In addition to the immediately realized impacts of phytoplankton and nutrient flushing, the loss of biota available for lacustrine recycling pathways may reduce the future availability of algal nutrients. Schulte and Lackey (1973) implicated flushing of phytoplankton and nutrients as a check on primary production in Claytor Lake, a main-stem hydropower reservoir in Virginia. The impact of increased outlet discharges on Claytor Lake phytoplankton was most pronounced in the downstream reservoir reaches.

Chlorophyll 'a' discharged through Libby Dam was used as an index of phytoplankton losses from Lake Koocanusa. In that chlorophyll 'a' determinations were not corrected for phaeopigments, they did not accurately represent losses of viable phytoplankton from the reservoir. The only year in which chlorophyll 'a' was analyzed over the sampling season was 1975. Chlorophyll 'a' concentrations discharged through Libby Dam in 1975 ranged from 0.20 to 6.7 mg m^{-3}, with a mean concentration of 1.85 mg m^{-3} (Fig. 13). Such a mean concentration was cited by Wetzel (1975) as characteristic of oligotrophic lakes. The large pulse of chlorophyll 'a' was discharged during March and April during drawdown and isothermy. In that a diatom bloom was likely during that period, a large loss of chlorophyll 'a' was plausible. There was a smaller pulse of chlorophyll 'a' during July and August while water was discharged

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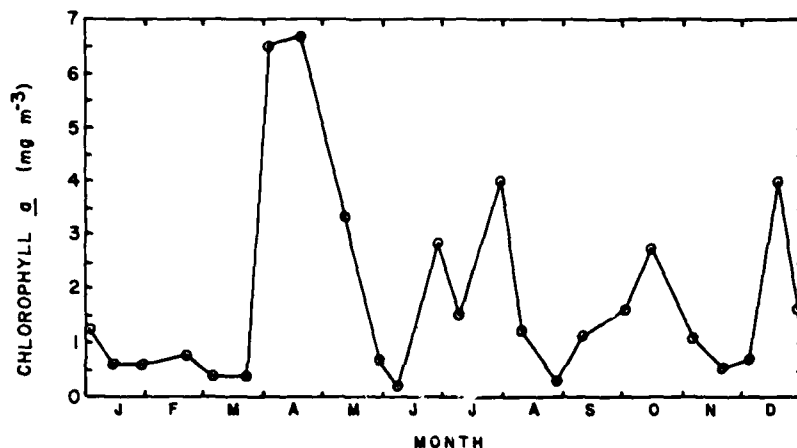
Figure 13. Chlorophyll 'a' concentrations during 1975
in the Kootenai River, 1.1 km downstream of Libby Dam.

through the spillway. The riverine concentrations of chlorophyll 'a'
were often greater than those measured at similar times at the Forebay
station; however, reservoir samples were taken within the euphotic zone
and, except for periods of spillway discharge, were not representative
of sluiceway discharges to the Kootenai River.

Nutrient limitation

Evidence from several sources suggests that primary productivity in
Lake Koocanusa was N-limited. An algal assay conducted on the reservoir
in June 1973 as part of the National Eutrophication Survey revealed

that potential primary productivity was high, but the control yields of
the assay algae, Selenastrum capricornutum, were N limited (U.S.
Environmental Protection Agency 1977). According to Wetzel's (1975)
criteria, Lake Koocanusa was ultraoligotrophic in that mean epilimnetic
concentrations of inorganic N did not exceed 0.02 mg L^{-1}. Mean
epilimnetic concentrations of dissolved P and dissolved ortho-P ranged
from 0.01 to 0.08 mg L^{-1}, thereby ranking Lake Koocanusa as meso-
eutrophic. The low concentrations of N were unexpected in
light of the potentially eutrophic loadings predicted by Bonde and Bush
(1975). The Environmental Protection Agency has used N:P mass ratios as
an index of nutrient limitation (Rast and Lee 1978). The N:P mass ratio
is the quotient of inorganic N over soluble ortho-P. A ratio of less
than 5:1 suggests N limitation, greater than 10:1 suggests P limitation,

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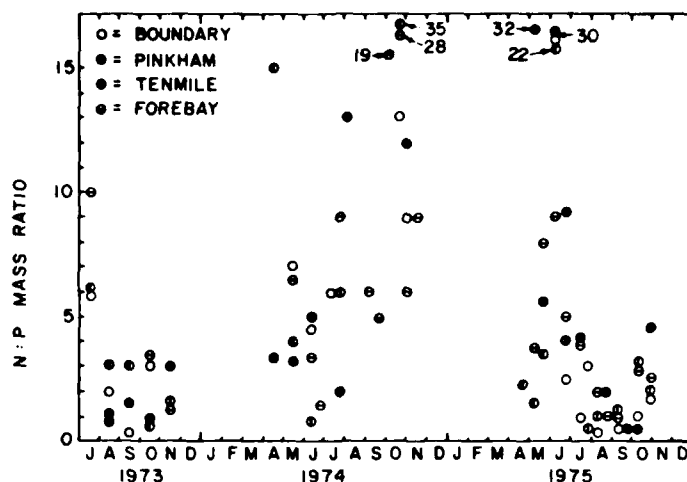
Figure 14. Mass ratios of inorganic N to soluble
ortho-P (N:P) for Lake Koocanusa, 1973 through
1975.

and between 5:1 and 10:1 either nutrient may be limiting. The N:P mass
ratios for Lake Koocanusa (Fig. 14) indicate N limitation in 1973 and a
tendency towards limitation by either nutrient in 1974 and 1975.

The usefulness of algal assay procedures, N:P mass ratios, and
nutrient concentrations for assessing nutritional limitation of phyto-
plankton productivity is seriously impaired because such assessments are
based upon in situ nutrient concentrations. The dynamics of uptake,
use, storage and excretion of nutrients by phytoplankton and microbial
remineralization rates are not adequately accounted for.

Sampling program critique

Some important assumptions and biases are inherent in the primary
production sampling programs conducted on Lake Koocanusa. The in situ
incubations used in the C-14 light and dark bottle method create an
artificial environment by isolating phytoplankton from turbulence and
circulation through light gradients. Harris and Lott (1973b) reported
that the photoinhibition observed during bottle incubations was not
present in phytoplankton subjected to vertical mixing. From this they
concluded that their in situ incubations underestimated actual primary
productivity. In situations where phytoplankton are circulated below
the euphotic zone, St. John et al. (1976) reasoned that in situ incuba-
tions within the euphotic zone would overestimate actual primary produc-
tivity. Although these two biases affected the Lake Koocanusa data,

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their overall impact on primary productivity estimates should have been lessened because of their opposite tendencies.

Questions exist over exactly what aspect of primary productivity the C-14 method measures: net, gross, or somewhere between. Golterman (1975) and Vollenweider (1974) assert that measurements from the generalized C-14 method may range from net to gross primary productivity and depend upon variables such as length of incubation, physiological state of the phytoplankton and environmental conditions affecting the phytoplankton. Wetzel (1975) concluded that estimates close to net primary productivity should result under many of the situations where the C-14 method is used. The C-14 methods prescribed by the U.S. Geological Survey (Greeson et al. 1977), American Public Health Association (1976), and Hall and Moll (1975) are taken as estimates of net primary productivity; the methods employed at Lake Koocanusa were essentially the same as described in these three publications.

The consensus is that the C-14 method measures only that portion of C assimilated into particulate organic C compounds within the cell; not measured is that portion of C assimilated into dissolved organic C compounds which have been excreted from the cell prior to measurement of radioactivity (Platt et al. 1975, Vollenweider 1974). Modifications of the C-14 method are available to estimate the production of extracellular products of photosynthesis (Vollenweider 1974, Hall and Moll 1975), but such modifications were not used in the sampling at Lake Koocanusa.

In light of the technical difficulties involved in the C-14 methodology, the artificial environments created by in situ incubations, and the ambiguity over what is actually measured by the C-14 method, it appears best to consider the results of the C-14 method as estimates of net primary production, with reliability no better than $\pm$ 50%.

Primary production sampling programs are further complicated by the patchy horizontal and vertical distributions characteristic of phytoplankton populations (Fogg 1975). Lake Koocanusa's plankton populations were transported horizontally and vertically throughout the lake by the hydrodynamics of reservoir operations and thus were mixed. A Kruskal-Wallis test (Zar 1974), an analysis of variance by ranks, was applied to each of the four years to test for significant differences in areal primary productivity among the four stations. Within each year only those time periods represented by samples at all four stations were tested. A

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chi square test with three degrees of freedom revealed the following probabilities: 0.63 for 1972, 0.43 for 1973, 0.03 for 1974 and 0.48 for 1975. No significant differences in areal primary productivity existed among the four stations. In retrospect, primary productivity may have been better assessed in Lake Koocanusa with more frequent and intensive samplings at fewer stations.

CONCLUSIONS

A major concern with Lake Koocanusa has been the discrepancy between the predicted and actual biological response to large loadings of N and P delivered by the Kootenai River. Bonde and Bush (1975) used a nutrient loading model to predict a potentially eutrophic reservoir; however, postimpoundment trophic status, based on primary productivity criteria, was oligotrophic. Rast and Lee (1978) noted that nutrient loading models may be inapplicable to water bodies possessing some of the following characteristics: short retention time, a lack of nutritional limitation of primary productivity, large volumes of stratified interflow or underflow, and high levels of abiogenic turbidity. Lake Koocanusa was subject, in varying degrees, to each of the above conditions.

The flood storage function of Lake Koocanusa, in conjunction with large seasonal inflows and withdrawals, resulted in large-scale fluctuations in volume and surface area. Such an operational schedule yielded mean annual retention times that ranged from 0.20 to 0.68 years. The complex reservoir hydrodynamics caused by this operational schedule resulted in a predominantly weak thermal structure in the reservoir.

A direct consequence of weak thermal structure was circulation of phytoplankton out of the euphotic zone. The decrease in phytoplankton photosynthesis caused by low light conditions beneath the euphotic zone was an important factor in the suppression of primary productivity to oligotrophic levels. Circulation effects on photosynthesis were further compounded by the highly turbid inflows received during spring filling. Euphotic zone depths were substantially reduced on occasion by the large amounts of suspended sediment in the reservoir's surface water. In that thermal structure was quite weak during filling, the shallowness of the euphotic zone meant that the reservoir's phytoplankton community spent much of its time below it during reservoir filling. The phytoplanktonic

light environment also was highly dependent upon seasonally and meteorologically induced variations in solar radiation. The major factor controlling primary productivity in Lake Koocanusa was the quantity of light received by phytoplankton; however, no one environmental variable fully accounted for the seasonal variations in primary productivity.

The potential for nutrient limitation of primary productivity was evident in the data, but in situ nutrient concentrations may not be the best measure of nutritional limitation. Abiotic and biotic materials were flushed from the reservoir by the large-scale water movements and there was a loss of net primary production that would have been otherwise available to the reservoir's trophic structure. Reductions in reservoir volume periodically exposed large areas of bottom. This precluded long term establishment of littoral and benthic flora and fauna in these exposed areas and hence reduced the production of organic matter by such communities.

The biology of newly impounded reservoirs can be expected to be dynamic. This is due, in large part, to the influx of nutrients from inundated terrestrial soils and the rapid spatial expansion of the aquatic environment. Such a dynamic biological response was coupled with the complex hydrodynamics of Lake Koocanusa. The result was a complex lacustrine ecosystem dominated by physical limnological processes.

Since September 1975 major changes have transpired that will likely affect the physical, chemical and biological limnology of Lake Koocanusa. Nutrient loadings to the reservoir have been substantially reduced because of wastewater treatment and reduced industrial pollution upstream of the reservoir since 1975. Reservoir hydrodynamics will likely be altered by power production which began in August 1975, and by the use of a selective withdrawal structure designed to draw water from selected depths for better control of downstream water quality. Still being contemplated is a partial diversion of the Kootenay River into the Columbia River near Canal Flats near British Columbia. The annual diversion of 1.85 km^3 would reduce by 30% the average flow of the Kootenay River at a point downstream of the St. Marys River and would substantially reduce minimum flows (Water Resources Services 1976). This diversion could cause significant changes in flood storage and power production at Lake Koocanusa. In light of these implemented or proposed alterations, it is

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strongly recommended that water quality data collected on the reservoir since 1975 be evaluated to better understand the aquatic environment of Lake Koocanusa and how it has responded or may respond to further environmental pertubation.

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APPENDIX A: WATER TEMPERATURES IN LAKE KOOCANUSA.
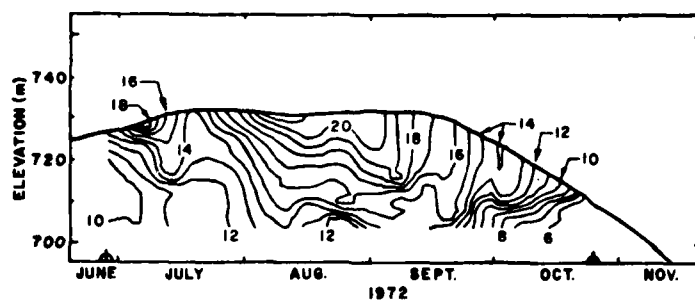
a. Boundary station.
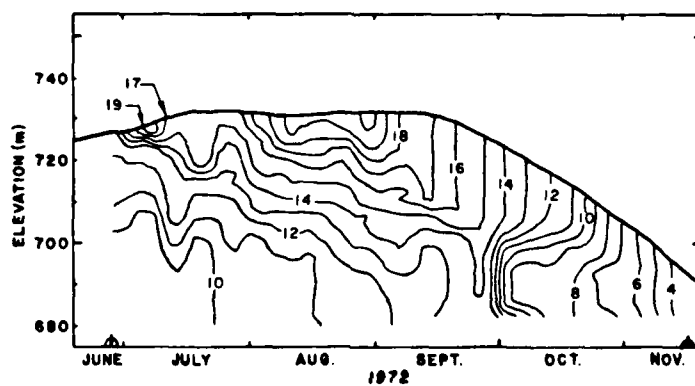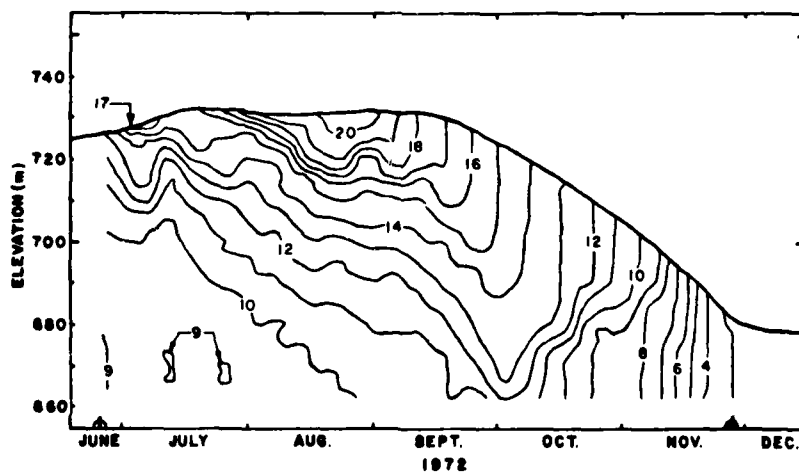
b. Pinkham station.

c. Tenmile station.

Figure A1. Isopleths of water temperature (°C) in 1972.

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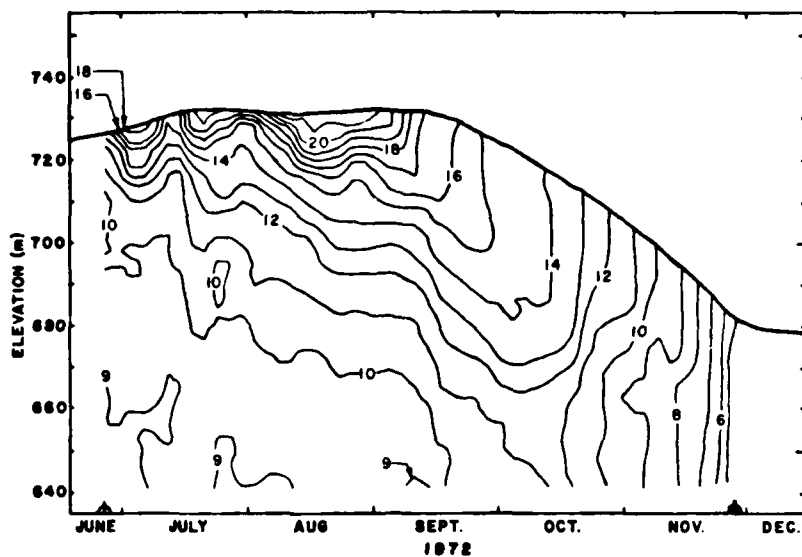
d. Forebay station.

Figure A1 (cont'd). Isopleths of water temperature (°C) in 1972.
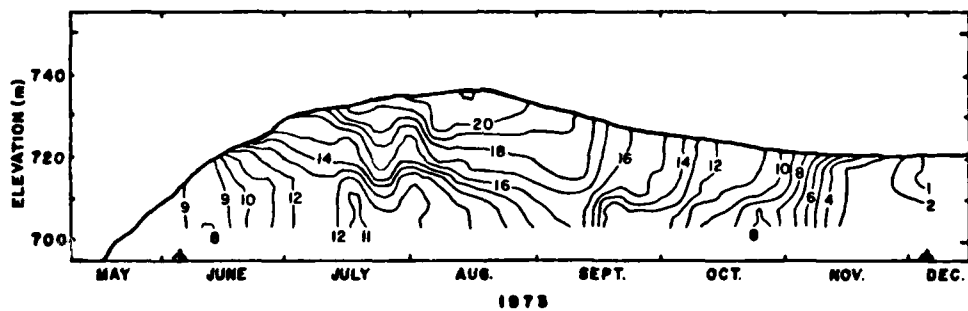
a. Boundary station.
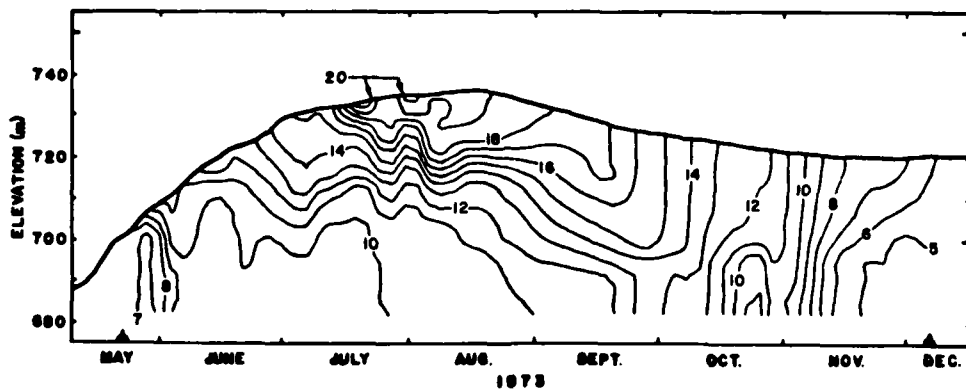
b. Pinkham station.

Figure A2. Isopleths of water temperature (°C) in 1973.
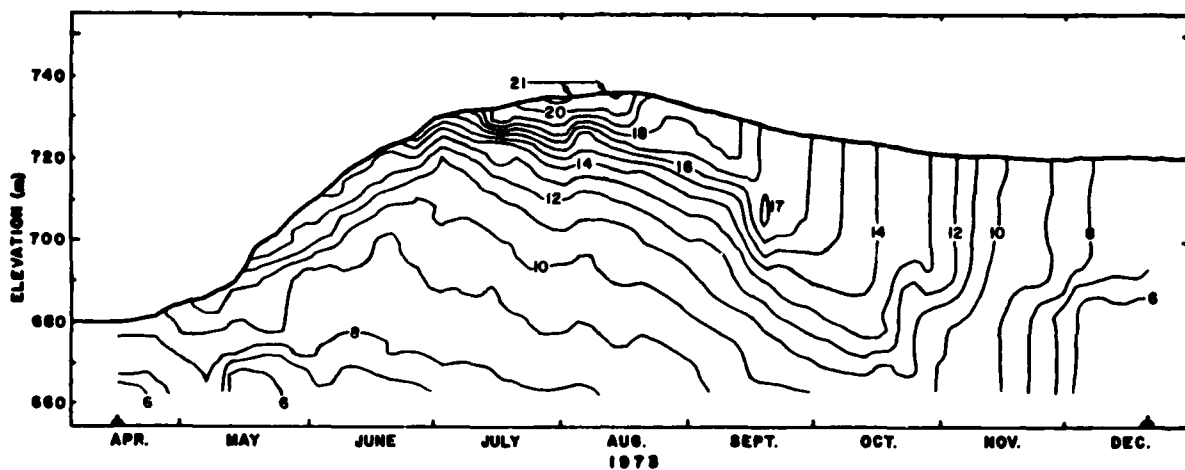
c.   Tenmile station.
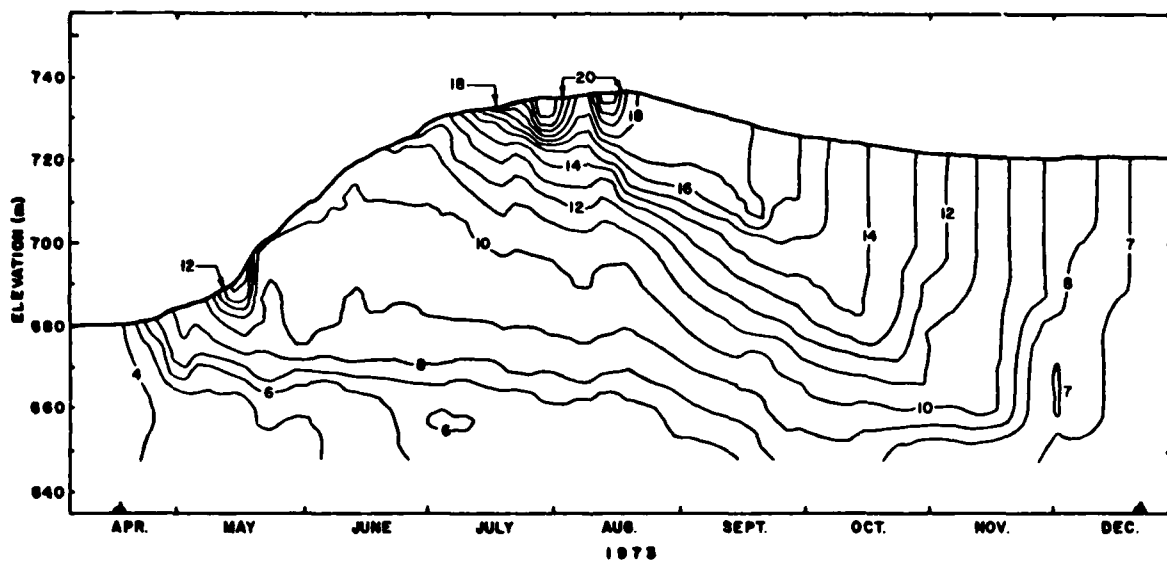
d.   Forebay station.

Figure A2   (cont'd).
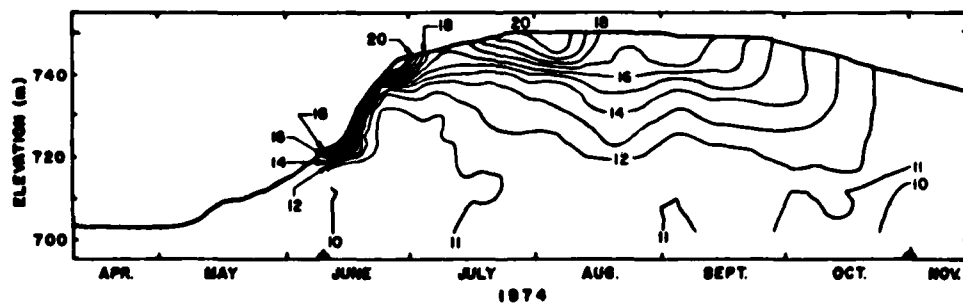
a.   Boundary station.

Figure A3.   Isopleths of water temperature (°C) in 1974.

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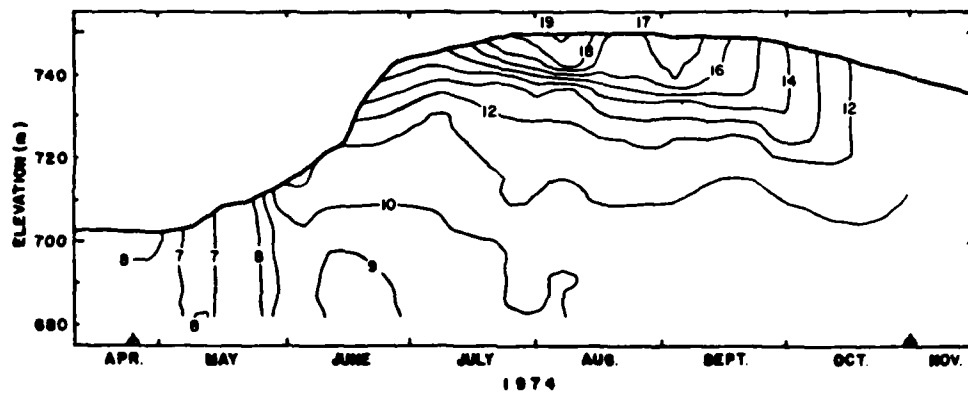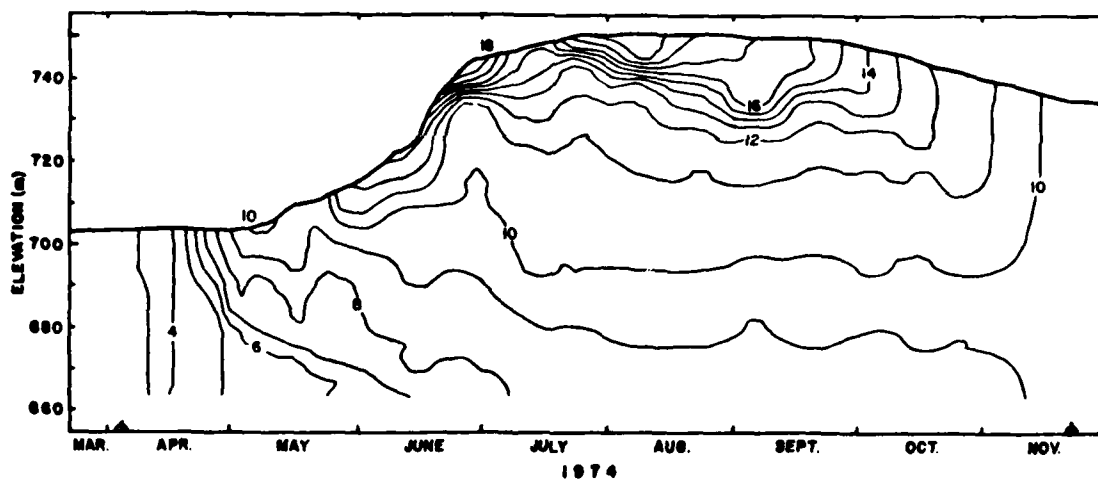
b. Pinkham station.

c. Tenmile station.

Figure A3 (cont'd). Isopleths of water temperature (°C) in 1974.
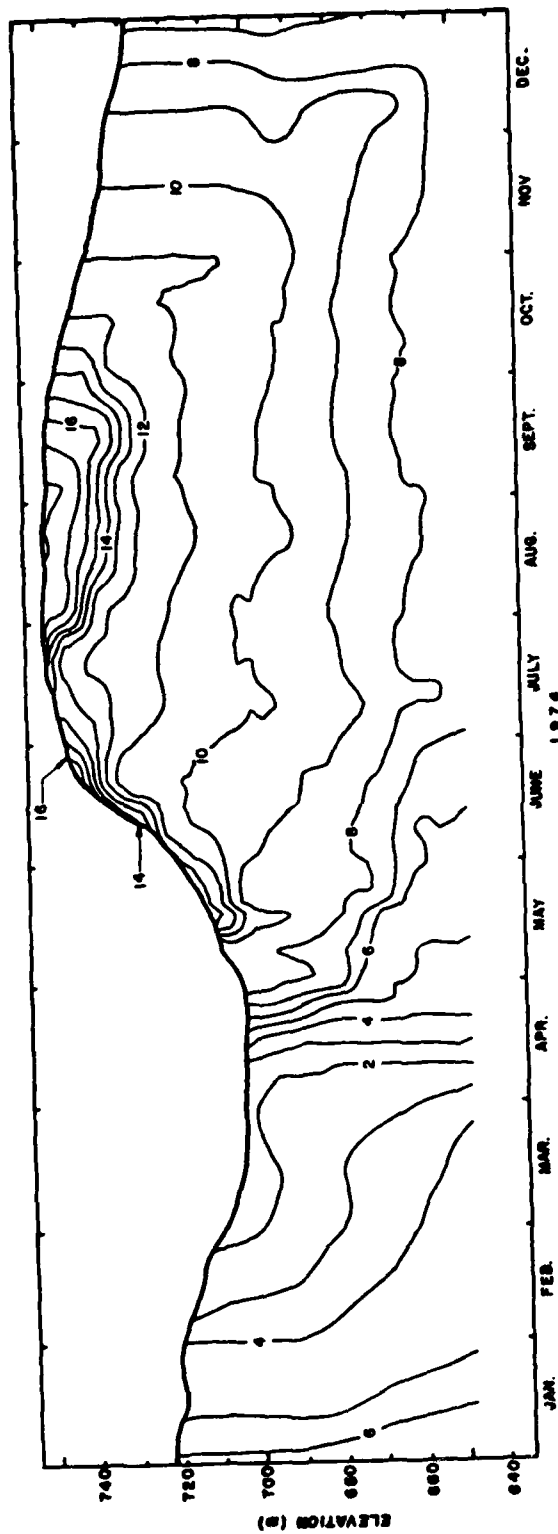
68

d. Forebay station.

Figure A3 (cont'd).

69
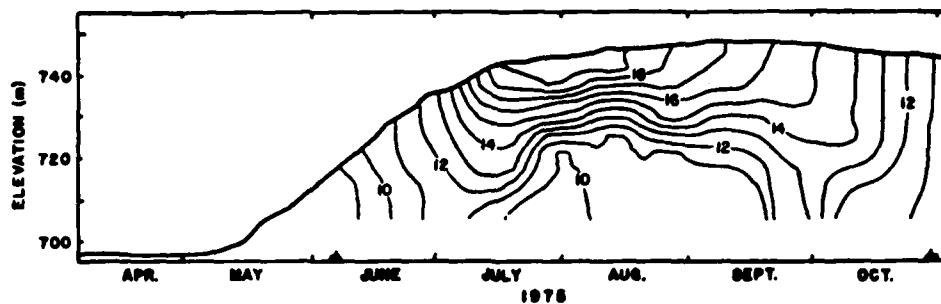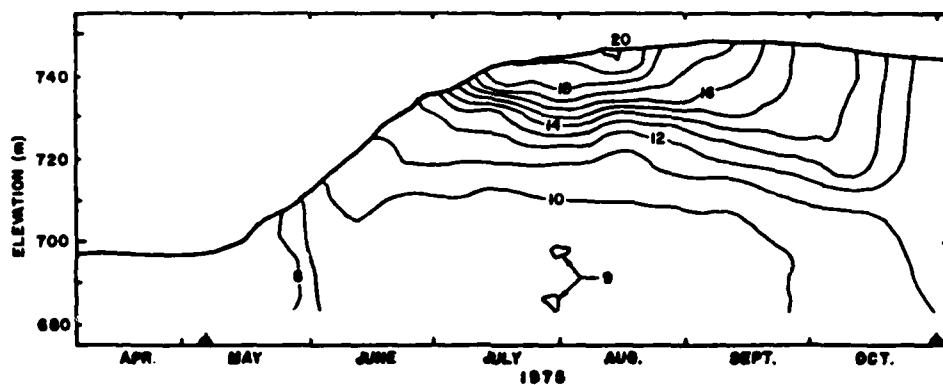
a. Boundary station.
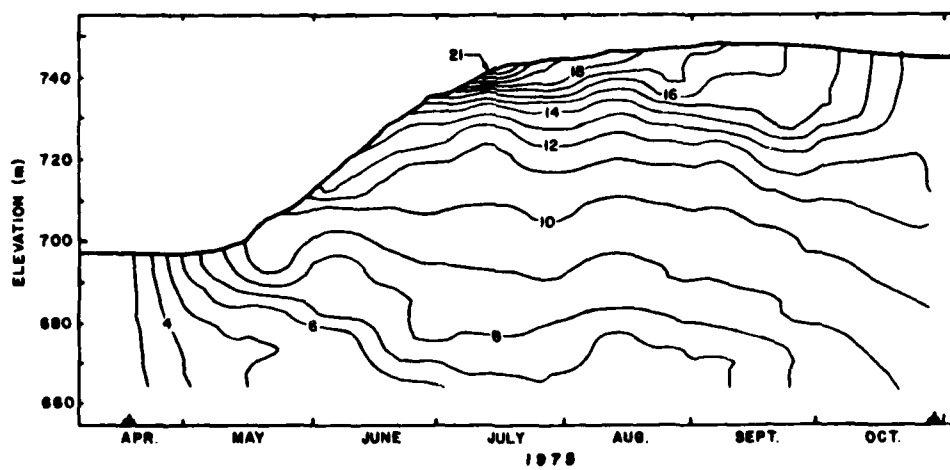
b. Pinkham station.

c. Tenmile station.

Figure A4. Isopleths of water temperature (°C) in 1975.

70
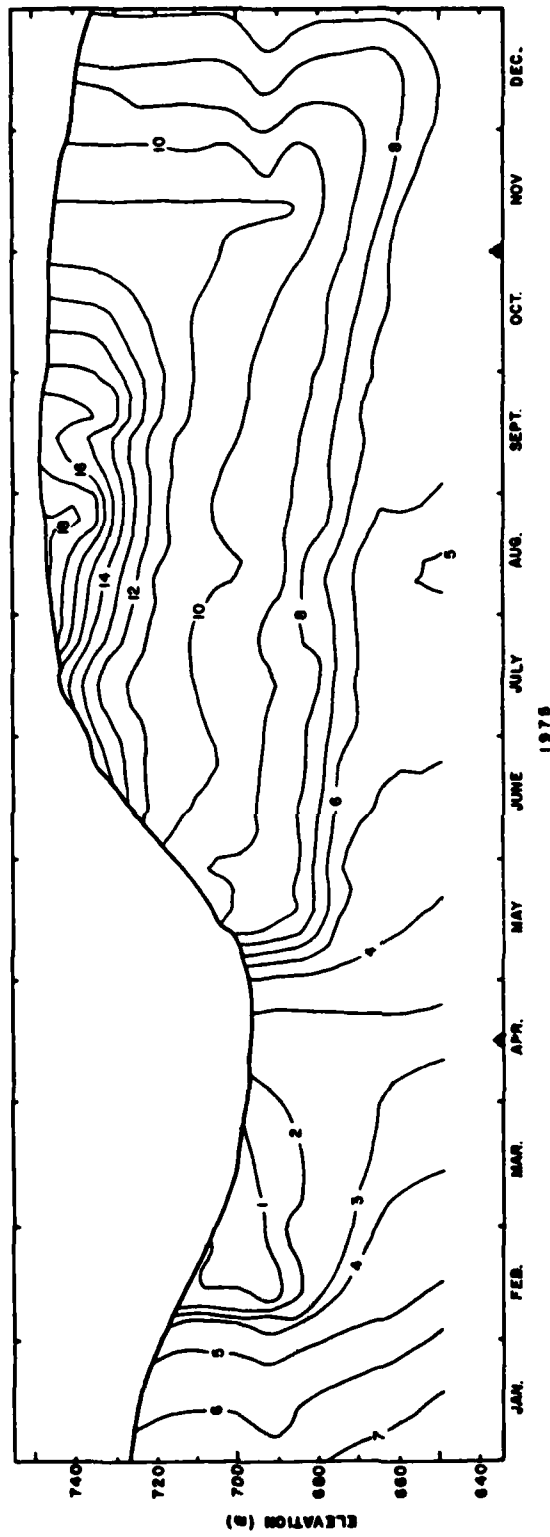
d. Forebay station.

Figure A4 (cont'd).

71
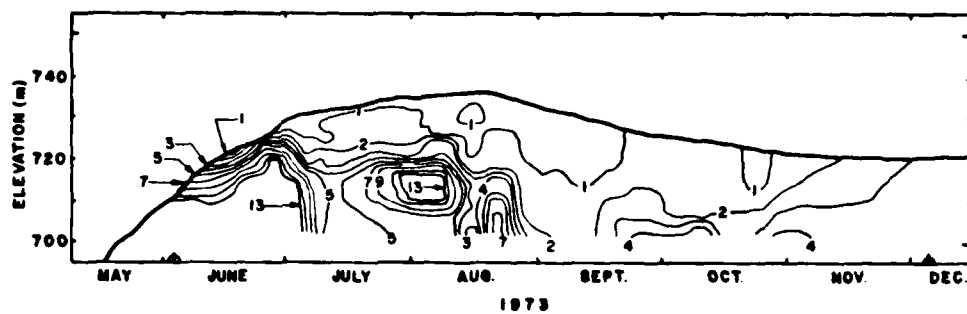
a. Boundary station.

b. Pinkham station.

c. Tenmile station.

Figure B1. Isopleths of extinction coefficients, 1973.
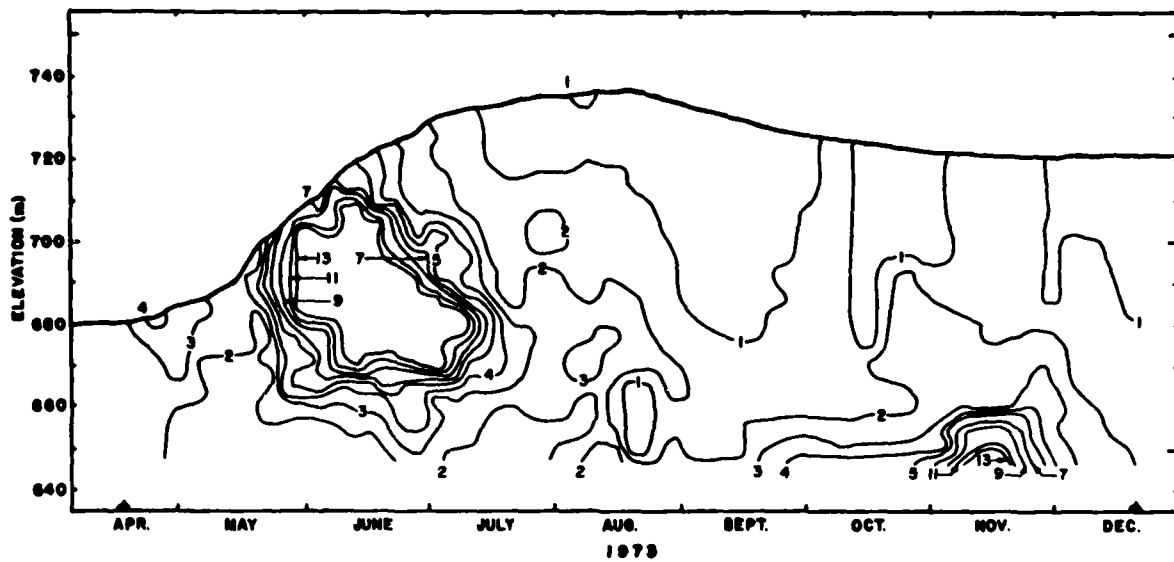
d. Forebay station.

Figure B1 (cont'd). Isopleths of extinction coefficients, 1973.
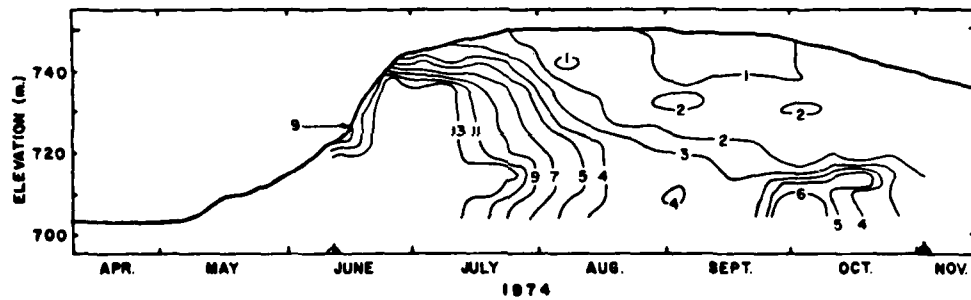
a. Boundary station.
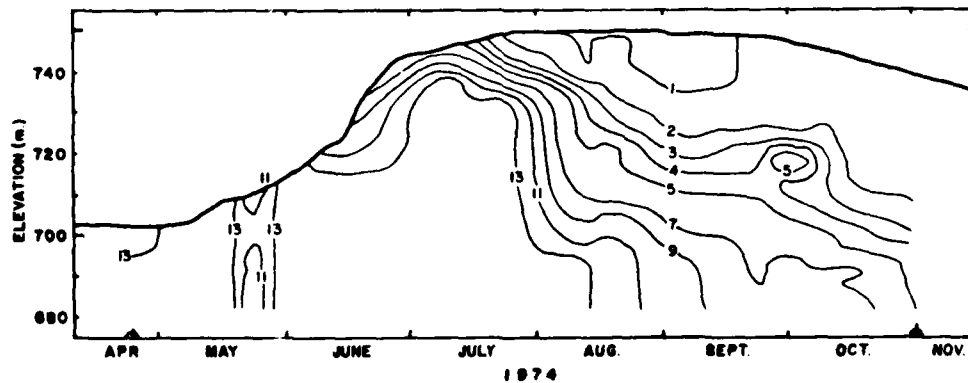
b. Pinkham station.

Figure B2. Isopleths of extinction coefficients, 1974.
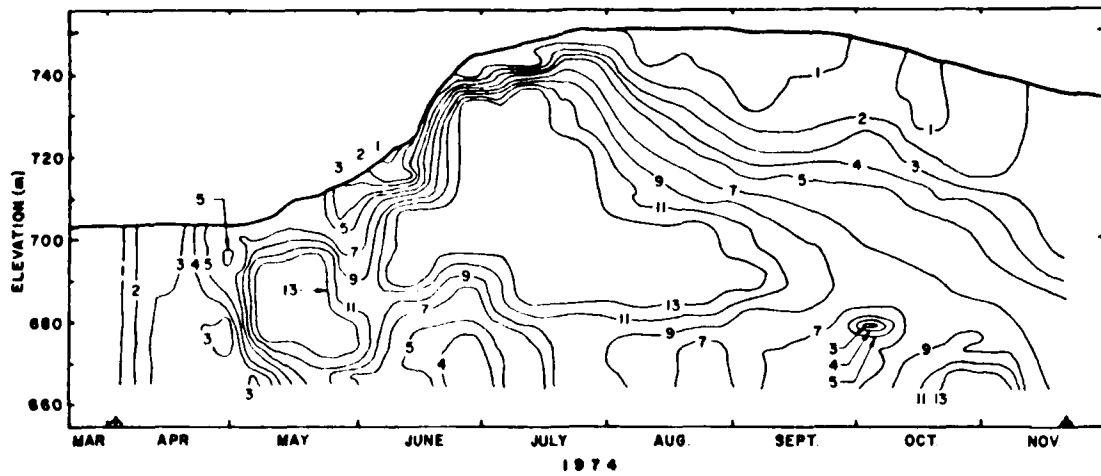
c. Tenmile station.
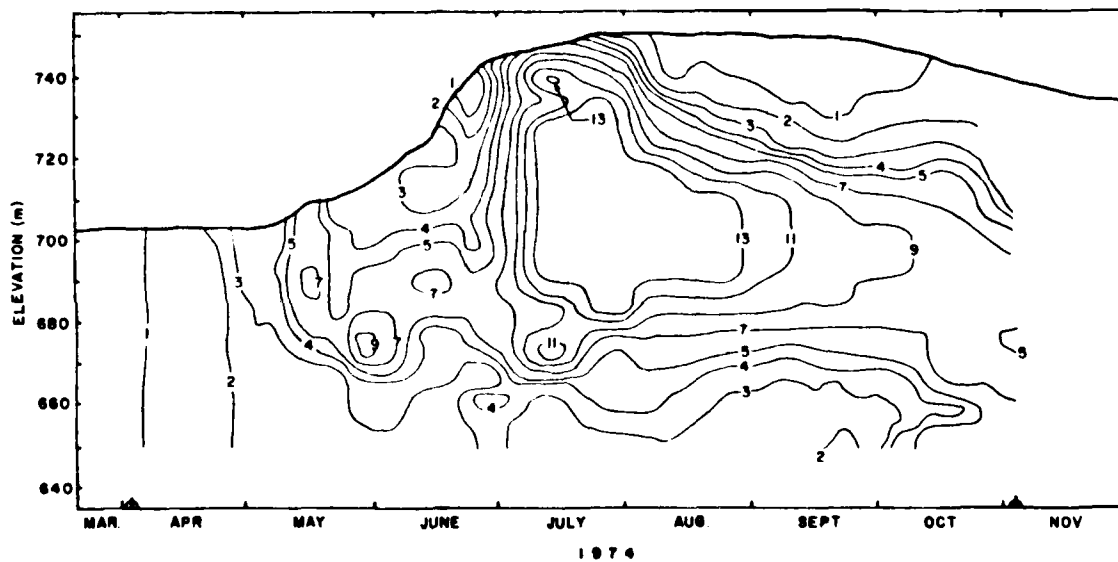
d. Forebay station.

Figure B2 (cont'd).
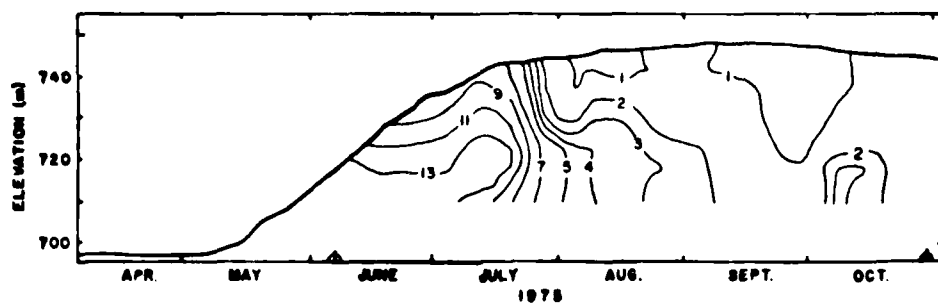
a. Boundary station.

Figure B3. Isopleths of extinction coefficients, 1975.

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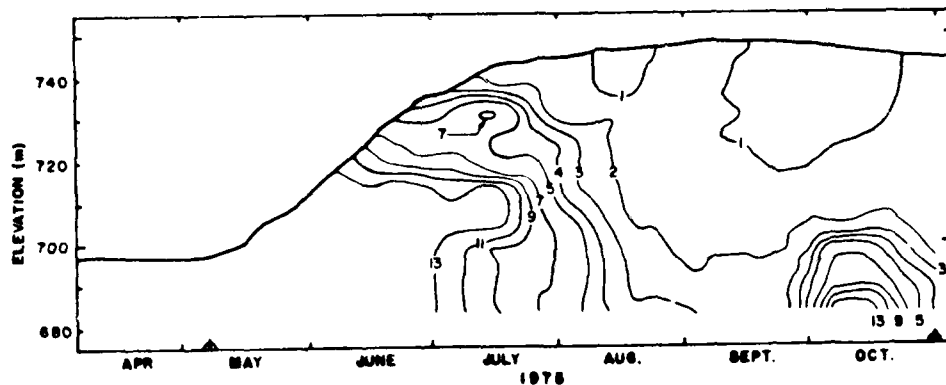
b. Pinkham station.
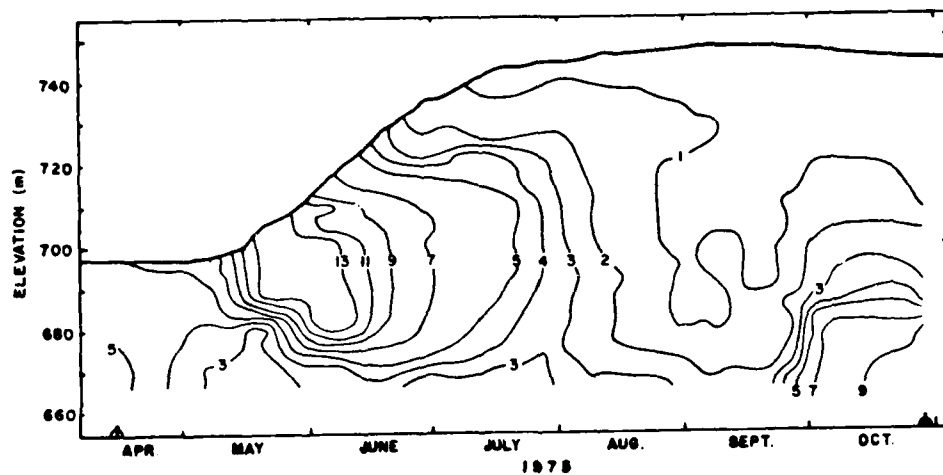
c. Tenmile station.
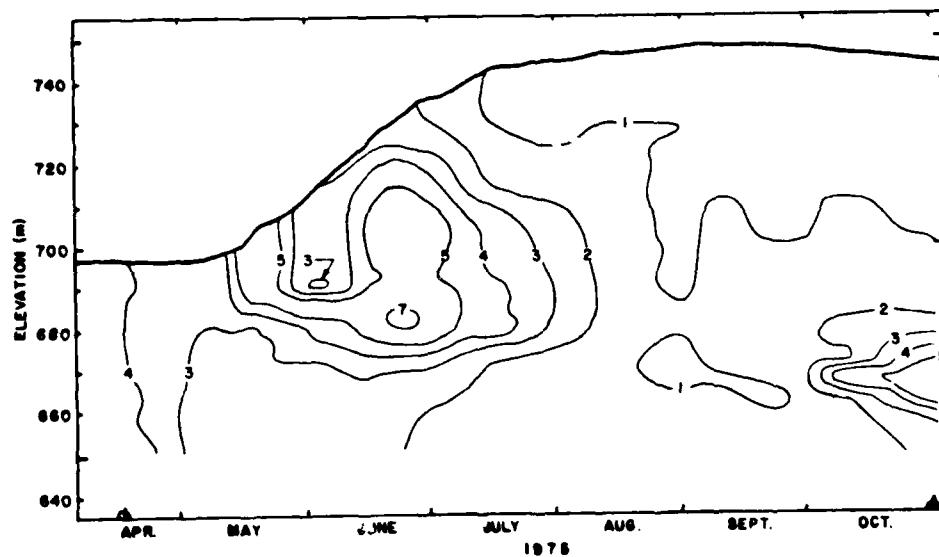
d. Forebay station.

Figure B3 (cont'd). Isopleths of extinction coefficients, 1975.

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APPENDIX C: NITROGEN AND PHOSPHORUS CONCENTRATIONS IN LAKE KOOCANUSA, 1972-75. Upper value in tables sampled 3.1 m below surface, lower value sampled 3.1 m above bottom.

Table C1. Boundary station, 1972.

| Date | Total | N as N (mg L^{-1}) | | Dissolved P as P (mg L^{-1}) |
		Dissolved NH$_3$	Dissolved NO$_2^-$ + NO$_3^-$	
6-14	0.19	--	0.07	0.02
	0.35	--	0.07	0.01
6-21	0.17	--	0.09	0.08
	0.20	--	0.10	0.12
6-28	0.25	0.04	0.02	0.09
	0.64	0.07	0.00	0.09
7-06	0.23	--	0.00	0.01
	0.19	--	0.05	0.04
7-13	0.08	--	0.00	0.02
	0.11	--	0.03	0.02
7-19	0.16	--	0.03	0.02
	0.15	--	0.04	0.03
7-27	0.27	0.03	0.01	0.03
	0.23	0.04	0.05	0.02
8-02	0.16	--	0.01	0.02
	0.10	--	0.03	0.02
8-09	0.05	--	0.00	0.00
	0.19	--	0.02	0.03
8-16	0.14	--	0.00	0.02
	0.13	--	0.04	0.04
8-23	0.18	--	0.01	0.02
	0.22	--	0.02	0.04
8-31	0.35	0.04	0.00	0.02
	0.27	0.00	0.02	0.05
9-06	0.18	--	0.01	0.02
	0.21	--	0.07	0.04
9-12	0.25	--	0.00	0.03
	0.18	--	0.04	0.03
9-21	0.35	--	0.00	0.03
	0.39	--	0.04	0.04
9-28	0.59	0.04	0.03	0.02
	0.51	0.03	0.03	0.02
10-03	0.26	--	0.00	0.00
	0.12	--	0.01	0.04
10-19	0.30	0.06	0.06	0.06
	0.29	0.05	0.09	0.07
Mean	0.23	0.04	0.02	0.03
	0.25	0.04	0.04	0.04
S.D.	0.12	0.01	0.03	0.02
	0.14	0.03	0.03	0.03

Table C2. Pinkham station, 1972.

| Date | Total | N as N (mg L^{-1}) | | Dissolved P as P (mg L^{-1}) |
		Dissolved NH$_3$	Dissolved NO$_2^-$ + NO$_3^-$	
6-14	0.35	--	0.07	0.02
	0.34	--	0.08	0.02
6-28	0.22	0.04	0.04	0.08
	0.27	0.04	0.05	0.08
7-13	0.09	--	0.00	0.02
	0.12	--	0.05	0.02
7-19	0.14	--	0.01	0.02
	0.22	--	0.07	0.04
8-02	0.03	--	0.00	0.02
	0.11	--	0.03	0.03
8-09	0.22	--	0.01	0.00
	0.16	--	0.04	0.01
8-16	0.14	--	0.00	0.01
	0.25	--	0.04	0.02
8-23	0.12	--	0.00	0.03
	0.24	--	0.03	0.04
8-30	0.33	0.03	0.02	0.02
	0.17	0.09	0.04	0.04
9-06	0.22	--	0.00	0.02
	0.57	--	0.12	0.04
9-27	0.23	0.04	0.03	0.02
	0.37	0.07	0.07	0.05
10-03	0.26	--	0.01	0.02
	0.27	--	0.01	0.04
10-18	0.12	0.05	0.00	0.05
	0.23	0.06	0.07	0.06
10-25	0.20	--	0.02	0.04
	0.26	--	0.06	0.05
11-01	0.34	--	0.04	0.02
	0.41	--	0.05	0.04
11-15	0.34	0.09	0.10	0.04
	0.26	0.07	0.10	0.05
Mean	0.21	0.05	0.02	0.03
	0.27	0.07	0.06	0.04
S.D.	0.10	0.02	0.03	0.02
	0.12	0.02	0.03	0.02

Table C3. Tenmile station, 1972.

Date	Total	N as N (mg L^{-1}) Dissolved NH_3	N as N (mg L^{-1}) Dissolved $NO_2^- + NO_3^-$	Dissolved P as P (mg L^{-1})
6-06	0.24	--	0.02	0.04
	0.33	--	0.13	0.04
6-13	0.14	--	0.02	0.06
	0.16	--	0.11	0.07
6-20	0.24	--	0.00	0.02
	0.30	--	0.07	0.05
6-27	0.23	0.10	0.00	0.04
	0.23	0.10	0.00	0.04
7-05	0.24	--	0.00	0.01
	0.33	--	0.06	0.02
7-12	0.25	--	0.05	0.03
	0.17	--	0.02	0.05
7-19	0.15	--	0.01	0.03
	0.35	--	0.10	0.03
7-25	0.14	0.01	0.00	0.01
	0.16	0.02	0.02	0.03
8-01	0.05	--	0.00	0.00
	0.16	--	0.06	0.04
8-08	0.37	--	0.00	0.02
	0.17	--	0.06	0.04
8-15	0.27	--	0.00	0.02
	0.19	--	0.08	0.03
8-22	0.23	--	0.00	0.01
	0.30	--	0.03	0.03
8-29	0.22	0.02	0.00	0.01
	0.21	0.04	0.04	0.04
9-05	0.21	--	0.00	0.01
	0.29	--	0.11	0.04
9-11	0.23	--	0.00	0.01
	0.31	--	0.12	0.03
9-18	0.14	--	0.00	0.03
	0.18	--	0.05	0.04
9-26	0.49	0.01	0.00	0.02
	0.19	0.01	0.03	0.03
10-02	0.16	--	0.00	0.01
	0.18	--	0.08	0.01
10-16	0.15	0.08	0.02	0.02
	0.18	0.07	0.06	0.04
10-24	0.11	--	0.01	0.03
	0.21	--	0.04	0.04

Table C3 (cont'd).

| Date | Total | N as N (mg L^{-1}) | | Dissolved P as P (mg L^{-1}) |
		Dissolved NH$_3$	Dissolved NO$_2^-$ + NO$_3^-$	
10-31	0.06	--	0.01	0.02
	0.36	--	0.03	0.04
11-06	0.17	--	0.01	0.02
	0.41	--	0.03	0.03
11-13	0.27	0.05	0.04	0.05
	0.19	0.05	0.07	0.05
11-21	0.32	--	0.13	0.03
	0.34	--	0.13	0.02
11-27	0.45	--	0.25	0.06
	0.42	--	0.11	0.06
Mean	0.22	0.04	0.02	0.02
	0.25	0.05	0.07	0.04
S.D.	0.11	0.04	0.05	0.02
	0.09	0.04	0.04	0.01

Table C4. Forebay station, 1972.

Date	Total	N as N (mg L^{-1}) Dissolved NH_3	N as N (mg L^{-1}) Dissolved $NO_2^- + NO_3^-$	Dissolved P as P (mg L^{-1})
6-05	0.38	--	0.13	0.06
	0.55	--	0.16	0.03
6-13	0.28	--	0.13	0.07
	0.34	--	0.19	0.07
6-20	0.31	--	0.00	0.04
	0.48	--	0.15	0.07
6-27	0.24	0.14	0.00	0.04
	0.36	0.11	0.11	0.05
7-05	0.22	--	0.01	0.01
	0.22	--	0.08	0.03
7-12	0.14	--	0.00	0.01
	0.13	--	0.00	0.06
7-18	0.17	--	0.00	0.02
	0.38	--	0.07	0.05
7-24	0.27	0.03	0.00	0.03
	0.18	0.05	0.00	0.03
8-01	0.09	--	0.00	0.00
	0.23	--	0.06	0.01
8-08	0.41	--	0.02	0.03
	0.42	--	0.11	0.04
8-15	0.17	--	0.00	0.01
	0.15	--	0.06	0.03
8-22	0.24	--	0.00	0.02
	0.27	--	0.06	0.04
8-28	0.04	0.02	0.01	0.01
	0.12	0.01	0.00	0.01
9-05	0.14	--	0.00	0.02
	0.36	--	0.09	0.05
9-11	0.20	--	0.00	0.02
	0.45	--	0.10	0.06
9-18	0.14	--	0.00	0.03
	0.16	--	0.05	0.06
9-25	0.30	0.07	0.00	0.04
	0.19	0.07	0.06	0.04
10-02	0.11	--	0.01	0.01
	0.17	--	0.08	0.02
10-10	0.20	--	0.01	0.03
	0.15	--	0.00	0.02
10-17	0.21	0.04	0.03	0.03
	0.27	0.06	0.09	0.04

Table C4 (cont'd).

| Date | Total | N as N (mg L^{-1}) | | Dissolved P as P (mg L^{-1}) |
		Dissolved NH$_3$	Dissolved NO$_2^-$ + NO$_3^-$	
10-24	0.18	--	0.03	0.03
	0.23	--	0.07	0.04
10-31	0.05	--	0.02	0.03
	0.05	--	0.04	0.04
11-06	0.22	--	0.02	0.02
	0.33	--	0.06	0.03
11-14	0.26	0.04	0.00	0.04
	0.25	0.06	0.01	0.07
11-21	0.21	--	0.08	0.05
	0.26	--	0.08	0.05
11-27	0.22	--	0.08	0.05
	0.30	--	0.09	0.04
Mean	0.21	0.06	0.02	0.03
	0.27	0.06	0.07	0.04
S.D.	0.09	0.05	0.04	0.02
	0.12	0.04	0.04	0.02

Table C5. Boundary station, 1973.

| Date | N as N (mg L^{-1}) | | | | Dissolved P as P (mg L^{-1}) |
	Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	
6-05	0.26	--	--	0.04	0.01
	0.17	--	--	0.03	0.01
6-12	0.17	--	--	0.01	0.03
	0.17	--	--	0.02	0.03
6-21	0.29	0.17	0.06	0.06	0.06
	0.18	0.09	0.01	0.08	0.04
6-28	0.37	--	--	0.02	0.06
	0.11	--	--	0.04	0.04
7-03	0.14	--	--	0.01	0.03
	0.13	--	--	0.02	0.04
7-10	0.17	--	--	0.02	0.03
	0.20	--	--	0.04	0.05
7-19	0.18	0.15	0.02	0.04	0.04
	0.27	0.14	0.05	0.08	0.04
7-24	0.24	--	--	0.03	0.03
	0.21	--	--	0.04	0.07
7-31	0.13	--	--	0.01	0.04
	0.25	--	--	0.11	0.05
8-07	--	--	--	0.00	0.04
	--	--	--	0.12	0.06
8-15	0.08	0.02	0.02	0.00	0.04
	0.21	0.06	0.02	0.09	0.07
8-21	0.27	--	--	0.02	0.00
	0.34	--	--	0.15	0.03
8-29	0.14	--	--	0.00	0.02
	0.17	--	--	0.02	0.12
9-05	0.10	--	--	0.00	0.04
	--	--	--	0.02	0.15
9-12	0.11	0.07	0.01	0.00	0.00
	0.13	0.08	0.03	0.00	0.06
9-18	0.04	--	--	0.00	0.07
	0.10	--	--	0.01	0.06
9-25	0.21	--	--	0.02	0.04
	0.22	--	--	0.03	0.05
10-03	0.11	0.05	0.04	0.02	0.09
	0.23	0.15	0.04	0.04	0.08
10-09	0.33	--	--	0.03	0.06
	0.24	--	--	0.02	0.05
10-15	0.29	--	--	0.05	0.07
	0.25	--	--	0.09	0.07
10-23	0.42	--	--	0.03	0.08
	0.44	--	--	0.11	0.12

Table C5 (cont'd).

| Date | N as N (mg L^{-1}) | | | | Dissolved P as P (mg L^{-1}) |
	Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	
10-30	0.24	--	--	0.07	0.20
	0.29	—	--	0.18	0.25
11-12	0.26	--	--	0.08	0.26
	0.28	—	--	0.07	0.28
12-04	0.26	--	--	0.13	0.06
	0.24	--	--	0.10	0.05
Mean	0.21	0.09	0.03	0.03	0.06
	0.22	0.10	0.03	0.06	0.08
S.D.	0.10	0.06	0.02	0.03	0.06
	0.08	0.04	0.02	0.05	0.07

Table C6. Pinkham station, 1973.

Date	N as N (mg L^{-1})				Dissolved P as P (mg L^{-1})
	Total N	Total organic N	Total $NH_3 + NH_4^+$	Dissolved $NO_2^- + NO_3^-$	
5-22	0.41	0.19	0.06	0.16	0.02
	0.36	0.10	0.08	0.17	0.02
5-30	0.21	--	--	0.08	0.02
	0.17	--	--	0.08	0.03
6-05	0.29	--	--	0.02	0.01
	0.22	--	--	0.04	0.02
6-12	0.23	--	--	0.01	0.03
	0.27	--	--	0.04	0.04
6-20	0.70	0.62	0.06	0.01	0.02
	0.23	0.16	0.02	0.05	0.03
6-28	0.17	--	--	0.01	0.02
	0.16	--	--	0.04	0.04
7-03	0.11	--	--	0.01	0.03
	0.20	--	--	0.03	0.05
7-10	0.16	--	--	0.00	0.02
	0.34	--	--	0.07	0.05
7-19	0.15	0.09	0.01	0.00	0.00
	0.18	0.03	0.01	0.10	0.02
7-24	0.16	--	--	0.01	0.02
	0.30	--	--	0.09	0.05
7-31	0.27	--	--	0.02	0.03
	0.24	--	--	0.12	0.04
8-07	--	--	--	0.03	0.03
	--	--	--	0.06	0.03
8-16	0.30	0.25	0.01	0.01	0.02
	0.34	0.23	0.00	0.17	0.04
8-21	0.16	--	--	0.01	0.00
	0.30	--	--	0.15	0.01
8-29	0.36	--	--	0.01	0.02
	0.52	--	--	0.31	0.03
9-05	0.23	--	--	0.11	0.04
	0.34	--	--	0.15	0.07
9-10	0.29	0.19	0.06	0.00	0.02
	0.26	0.10	0.01	0.15	0.05
9-18	0.15	--	--	0.00	0.07
	0.37	--	--	0.16	0.10
9-25	0.16	--	--	0.02	0.05
	0.22	--	--	0.03	0.05
10-04	0.25	0.20	0.04	0.01	0.03
	0.29	0.23	0.03	0.03	0.03
10-09	0.16	--	--	0.01	0.05
	0.10	--	--	0.06	0.05
10-15	0.18	--	--	0.03	0.05
	0.30	--	--	0.03	0.06

Table C6 (cont'd).

| Date | N as N ($mg\ L^{-1}$) | | | | Dissolved P as P ($mg\ L^{-1}$) |
	Total N	Total organic N	Total $NH_3 + NH_4^+$	Dissolved $NO_2^- + NO_3^-$	
10-23	0.23	--	--	0.02	0.06
	0.26	--	--	0.05	0.10
10-30	0.13	--	--	0.03	0.20
	--	--	--	0.03	0.27
11-12	0.23	--	--	0.03	0.12
	0.37	--	--	0.04	0.18
11-30	0.26	0.14	0.01	0.11	0.09
	0.24	0.11	0.03	0.07	0.10
12-04	0.14	--	--	0.06	0.04
	0.18	--	--	0.06	0.06
Mean	0.23	0.24	0.04	0.03	0.04
	0.27	0.14	0.03	0.09	0.06
S.D.	0.12	0.17	0.03	0.04	0.04
	0.09	0.07	0.03	0.07	0.05

Table C7. Tenmile station, 1973.

| | N as N (mg L^{-1}) | | | | Dissolved |
Date	Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	P as P (mg L^{-1})
3-14	0.32	0.02	0.09	0.21	0.31
	0.42	0.06	0.13	0.23	0.19
4-16	0.13	--	--	0.00	0.04
	0.26	--	--	0.01	0.05
4-25	0.18	0.12	0.02	0.04	0.06
	0.26	0.16	0.03	0.05	0.12
4-30	0.17	--	--	0.00	0.05
	0.22	--	--	0.04	0.05
5-07	0.37	--	--	0.00	0.04
	0.21	--	--	0.03	0.06
5-14	0.25	--	--	0.06	0.05
	0.26	--	--	0.09	0.06
5-23	0.24	0.17	0.03	0.01	0.05
	0.21	0.09	0.00	0.08	0.06
5-29	0.25	--	--	0.00	0.03
	0.30	--	--	0.16	0.04
6-04	0.25	--	--	0.00	0.03
	0.24	--	--	0.07	0.02
6-11	0.39	--	--	0.00	0.02
	0.35	--	--	0.13	0.04
6-19	0.23	0.21	0.01	0.01	0.01
	0.35	0.21	0.00	0.14	0.03
6-27	0.26	--	--	0.00	0.02
	0.26	--	--	0.13	0.04
7-02	0.17	--	--	0.00	0.02
	0.24	--	--	0.07	0.03
7-09	0.17	--	--	0.00	0.01
	0.28	--	--	0.12	0.03
7-17	0.31	0.25	0.06	0.00	0.01
	0.11	--	0.09	0.10	0.03
7-23	0.27	--	--	0.00	0.01
	0.35	--	--	0.13	0.03
7-30	0.20	--	--	0.00	0.02
	0.34	--	--	0.13	0.04
8-06	0.10	--	--	0.00	0.01
	--	--	--	0.12	0.04
8-14	0.13	0.09	0.02	0.01	0.02
	0.99	0.78	0.02	0.19	0.05
8-20	0.20	--	--	0.02	0.00
	0.36	--	--	0.17	0.02
8-28	0.14	--	--	0.04	0.00
	0.27	--	--	0.21	0.00
9-04	0.19	--	--	0.02	0.04
	0.28	--	--	0.19	0.06

Table C7 (cont'd).

	N as N (mg L^{-1})				Dissolved
	Total	Total organic	Total	Dissolved	P as P
Date	N	N	$NH_3 + NH_4^+$	$NO_2^- + NO_3^-$	(mg L^{-1})
9-14	0.17	0.13	0.03	0.00	0.03
	0.27	0.08	0.04	0.13	0.03
9-17	0.31	--	--	0.20	0.00
	0.28	--	--	0.17	0.02
9-24	0.05	--	--	0.01	0.05
	0.20	--	--	0.15	0.05
10-02	0.20	0.15	0.03	0.01	0.08
	0.34	0.17	0.00	0.14	0.10
10-10	0.07	--	--	0.02	0.05
	0.15	--	--	0.08	0.07
10-16	0.10	--	--	0.02	0.05
	0.41	--	--	0.19	0.07
10-24	0.51	--	--	0.12	0.03
	0.28	--	--	0.03	0.04
10-29	0.36	--	--	0.04	0.06
	0.35	--	--	0.08	0.07
11-13	0.17	--	--	0.05	0.06
	0.07	--	--	0.03	0.05
11-29	0.26	0.16	0.02	0.06	0.05
	0.26	0.14	0.04	0.07	0.10
12-05	0.26	--	--	0.06	0.06
	0.38	--	--	0.08	0.06
12-19	0.23	--	--	0.06	0.05
	0.33	--	--	0.04	0.07
Mean	0.22	0.14	0.03	0.03	0.04
	0.30	0.21	0.04	0.11	0.05
S.D.	0.10	0.07	0.03	0.05	0.05
	0.15	0.24	0.04	0.06	0.03

Table C8. Forebay station, 1973.

Date	N as N (mg L^{-1})				Dissolved P as P (mg L^{-1})
	Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	
4-17	0.28	--	--	0.06	0.14
	0.32	--	--	0.07	0.10
4-24	0.33	0.28	0.04	0.01	0.06
	0.30	0.04	0.13	0.13	0.10
4-30	0.35	--	--	0.01	0.04
	0.25	--	--	0.07	0.11
5-07	0.16	--	--	0.01	0.04
	0.44	--	--	0.06	0.11
5-14	0.17	--	--	0.00	0.03
	1.28	--	--	0.10	0.10
5-21	0.17	0.11	0.01	0.05	0.05
	0.23	0.13	0.00	0.10	0.09
5-29	0.20	--	--	0.04	0.08
	0.19	--	--	0.06	0.11
6-04	0.17	--	--	0.03	0.03
	0.19	--	--	0.05	0.08
6-11	0.31	--	--	0.11	0.04
	0.23	--	--	0.11	0.08
6-18	0.29	0.20	0.04	0.04	0.03
	0.38	0.20	0.02	0.16	0.07
6-27	0.16	--	--	0.00	0.02
	0.26	--	--	0.10	0.06
7-02	0.19	--	--	0.00	0.02
	0.22	--	--	0.06	0.08
7-09	0.15	--	--	0.03	0.01
	0.28	--	--	0.12	0.06
7-16	0.24	0.14	0.03	0.07	0.01
	0.43	0.16	0.06	0.21	0.05
7-23	0.30	--	--	0.03	0.00
	0.42	--	--	0.17	0.06
7-30	0.16	--	--	0.03	0.02
	0.40	--	--	0.21	0.08
8-06	0.11	--	--	0.00	0.00
	0.32	--	--	0.22	0.06
8-13	0.12	0.11	0.01	0.00	0.01
	0.62	0.37	0.01	0.20	0.07
8-20	0.50	--	--	0.28	0.09
	0.28	--	--	0.08	0.00
8-28	0.09	--	--	0.01	0.00
	0.71	--	--	0.31	0.07
9-04	0.15	--	--	0.03	0.04
	0.37	--	--	0.27	0.08
9-13	0.04	--	0.04	0.00	0.05
	0.34	0.05	0.03	0.23	0.03

Table C8 (cont'd).

Date	N as N (mg L^{-1}) Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Dissolved P as P (mg L^{-1})
9-17	0.11	--	--	0.01	0.00
	0.38	--	--	0.23	0.10
9-24	0.15	--	--	0.02	0.04
	0.29	--	--	0.22	0.08
10-01	0.11	0.01	0.09	0.01	0.05
	0.27	0.04	0.09	0.14	0.04
10-10	0.14	--	--	0.01	0.05
	0.06	--	--	0.08	0.06
10-16	0.17	--	--	0.03	0.07
	0.41	--	--	0.21	0.08
10-24	0.36	--	--	0.18	0.04
	0.42	--	--	0.23	0.03
10-29	0.16	--	--	0.08	0.08
	0.38	--	--	0.22	0.08
11-13	1.8	--	--	0.05	0.06
	0.27	--	--	0.16	0.08
11-28	0.28	0.14	0.01	0.04	0.05
	0.27	0.17	0.02	0.04	0.06
12-05	0.31	--	--	0.05	0.06
	0.29	--	--	0.08	0.07
12-19	0.26	--	--	0.04	0.07
	0.24	--	--	0.05	0.05
Mean	0.26	0.14	0.03	).04	0.04
	0.33	0.15	0.05	0.14	0.07
S.D.	0.29	0.08	0.03	0.06	0.03
	0.12	0.11	0.05	0.08	0.02

Table C9. Boundary station, 1974.

Date	N as N (mg L^{-1})			P as P (mg L^{-1})	
	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Total P	Dissolved ortho-P
6-12	0.29	0.01	0.08	0.07	0.02
	1.3	0.01	0.07	0.08	0.02
6-25	0.79	0.02	0.01	0.11	0.00
	0.28	0.03	0.03	0.16	0.01
7-09	0.22	0.03	0.03	0.02	0.01
	0.12	0.05	0.04	0.04	0.01
7-23	0.06	0.02	0.00	0.03	0.00
	0.04	0.02	0.01	0.03	0.01
8-06	0.30	0.02	0.00	0.01	0.00
	0.14	0.00	0.02	0.03	0.00
8-20	0.09	0.47	0.00	0.04	0.00
	0.08	0.34	0.03	0.06	0.00
9-04	0.21	0.03	0.03	0.06	0.00
	0.06	0.24	0.08	0.07	0.01
9-17	0.17	0.03	0.01	0.01	0.00
	0.16	0.04	0.09	0.05	0.00
10-02	0.03	0.22	0.00	0.01	0.00
	0.01	0.07	0.03	0.03	0.00
10-17	0.03	0.13	0.00	0.01	0.01
	0.06	0.12	0.00	0.02	0.00
10-31	0.08	0.08	0.01	--	0.01
	0.15	0.10	0.03	--	0.01
Mean	0.21	0.10	0.02	0.04	0.01
	0.22	0.09	0.04	0.06	0.01
S.D.	0.22	0.14	0.02	0.03	0.01
	0.37	0.11	0.03	0.04	0.01

Table C10. Pinkham station, 1974.

Date	N as N (mg L^{-1})				P as P (mg L^{-1})	
	Total N	Total organic N	Total $NH_3 + NH_4^+$	Dissolved $NO_2^- + NO_3^-$	Total P	Dissolved ortho-P
4-24	0.46	0.33	0.08	0.05	--	0.04
	0.40	0.20	0.11	0.09	--	0.04
5-03	0.26	--	--	0.15	--	--
	0.23	--	--	0.13	--	--
5-09	0.36	--	--	0.12	--	--
	0.30	--	--	0.10	--	--
5-17	0.37	--	--	0.14	--	--
	--	--	--	0.14	--	--
5-22	0.31	0.09	0.08	0.14	--	0.07
	0.29	0.07	0.10	0.13	--	0.07
5-30	0.24	--	--	0.12	--	--
	0.30	--	--	0.15	--	--
6-11	--	0.28	0.02	0.08	0.07	0.02
	--	0.23	0.01	0.07	0.02	0.02
7-10	--	0.01	0.12	0.00	0.07	0.00
	--	0.15	0.03	0.00	0.12	0.00
7-24	--	0.07	0.02	0.00	0.02	0.00
	--	0.06	0.03	0.05	0.06	0.01
8-07	--	0.09	0.10	0.03	0.02	0.01
	--	0.29	0.07	0.07	0.06	0.01
8-21	--	0.03	0.11	0.01	0.01	0.00
	--	0.01	0.13	0.12	0.04	0.01
9-05	--	0.10	0.04	0.00	0.03	0.00
	--	0.06	0.12	0.11	0.07	0.00
9-18	--	0.03	0.24	0.01	0.00	0.00
	--	0.17	0.10	0.09	0.04	0.01
10-01	--	0.04	0.04	0.51	0.06	0.00
	--	0.03	0.03	0.30	0.06	0.03
10-16	--	0.14	0.07	0.01	0.02	0.00
	--	0.10	0.07	0.10	0.04	0.01
10-30	--	0.01	0.09	0.03	0.00	0.01
	--	0.02	0.10	0.02	0.01	0.01
Mean	0.33	0.10	0.08	0.00	0.03	0.01
	0.30	0.12	0.08	0.10	0.05	0.02
S.D.	0.08	0.10	0.06	0.13	0.03	0.02
	0.06	0.09	0.04	0.07	0.03	0.02

Table C11. Tenmile station, 1974.

| Date | N as N (mg L^{-1}) | | | | P as P (mg L^{-1}) | |
	Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Total P	Dissolved ortho-P
4-03	0.33	--	--	0.03	--	--
	0.37	--	--	0.03	--	--
4-10	0.54	--	--	0.13	--	--
	0.44	--	--	0.20	--	--
4-17	--	--	--	0.08	--	--
	0.27	--	--	0.04	--	--
4-25	0.29	0.16	0.08	0.07	--	0.01
	0.26	0.09	0.12	0.04	--	0.08
5-02	0.22	--	--	0.08	--	--
	0.30	--	--	0.05	--	--
5-08	0.32	--	--	0.05	--	--
	1.2	--	--	0.09	--	--
5-16	0.17	--	--	0.03	--	--
	0.31	--	--	0.07	--	--
5-23	0.28	0.16	0.04	0.08	--	0.03
	0.37	0.10	0.12	0.13	--	0.04
5-29	0.52	--	--	0.02	--	--
	0.58	--	--	0.12	--	--
6-13	--	0.32	0.07	0.03	0.13	0.13
	--	0.20	0.12	0.47	0.15	0.15
6-27	--	0.11	0.01	0.00	0.02	0.00
	--	0.10	0.07	0.14	0.11	0.01
7-11	--	0.01	0.12	0.00	0.04	0.00
	--	0.16	0.03	0.13	0.07	0.02
7-25	--	0.14	0.05	0.01	0.02	0.01
	--	0.09	0.06	0.13	0.06	0.03
8-08	--	0.16	0.12	0.01	0.03	0.00
	--	0.16	0.04	0.13	0.07	0.01
8-22	--	0.06	0.18	0.01	0.01	0.00
	--	0.02	0.07	0.17	0.06	0.01
9-03	--	0.17	0.93	0.03	0.00	0.00
	--	0.12	0.35	0.17	0.06	0.01
9-19	--	0.07	0.03	0.01	0.04	0.00
	--	0.00	0.10	0.20	0.06	0.01
10-03	--	0.07	0.01	0.00	0.02	0.00
	--	0.11	0.01	0.13	0.07	0.01
10-15	--	0.01	0.35	0.00	0.00	0.01
	--	0.10	0.04	0.22	0.05	0.03
10-29	--	0.00	0.10	0.03	0.02	0.00
	--	0.01	0.10	0.23	0.08	0.01
11-19	--	0.07	0.05	0.07	0.02	0.00
	--	0.01	0.03	0.07	0.02	0.00
Mean	0.33	0.11	0.15	0.04	0.03	0.01
	0.46	0.09	0.09	0.14	0.07	0.0
S.D.	0.13	0.09	0.24	0.04	0.03	0.0
	0.30	0.06	0.08	0.10	0.03	0.0

Table C12. Forebay station, 1974.

Date	N as N (mg L^{-1})				P as P (mg L^{-1})	
	Total N	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Total P	Dissolved ortho-P
4-03	0.36	--	--	0.10	--	--
	0.29	--	--	0.04	--	--
4-10	0.32	--	--	0.12	--	--
	0.41	--	--	0.13	--	--
4-17	0.22	--	--	0.13	--	--
	0.25	--	--	0.13	--	--
4-23	0.34	0.22	0.02	0.08	--	0.00
	0.30	0.13	0.04	0.10	--	0.04
5-02	0.19	--	--	0.03	--	--
	0.23	--	--	0.10	--	--
5-08	0.23	--	--	0.06	--	--
	0.30	--	--	0.10	--	--
5-16	0.27	--	--	0.06	--	--
	0.27	--	--	0.08	--	--
5-21	0.30	0.13	0.06	0.08	--	0.02
	0.26	0.12	0.08	0.06	--	0.08˙
5-29	0.58	--	--	0.03	--	--
	0.61	--	--	0.09	--	--
6-14	--	0.23	0.07	0.03	0.05	0.03
	--	0.18	0.06	0.13	0.10	0.05
6-28	--	0.33	0.02	0.01	0.06	0.02
	--	0.00	0.08	0.18	--	0.05
7-12	--	0.16	0.07	0.00	0.04	0.00
	--	0.07	0.12	0.15	0.07	0.04
7-26	--	0.00	0.08	0.01	0.04	0.01
	--	0.01	0.08	0.14	0.09	0.00
8-09	--	0.16	0.04	0.00	0.01	0.00
	--	0.17	0.06	0.04	0.06	0.01
8-23	--	0.01	0.05	0.01	0.01	0.00
	--	0.01	0.05	0.19	0.07	0.03
9-06	--	0.27	0.05	0.13	0.09	0.03
	--	0.25	0.04	0.09	0.08	0.00
9-20	--	0.09	0.04	0.01	0.01	0.01
	--	0.03	0.16	0.20	0.08	0.05
10-04	--	0.23	0.01	0.18	0.01	0.01
	--	0.19	0.72	0.00	0.08	0.00
10-18	--	0.02	0.27	0.01	0.00	0.01
	--	0.05	0.40	0.23	0.08	0.06
11-01	--	0.06	0.03	0.03	0.00	0.01
	--	0.08	0.04	0.20	0.07	0.05
11-20	--	0.27	0.02	0.07	0.03	0.01
	--	0.15	0.05	0.22	0.08	0.04
Mean	0.31	0.16	0.06	0.06	0.03	0.01
	0.32	0.10	0.14	0.12	0.08	0.04
S.D.	0.12	0.11	0.06	0.05	0.03	0.01
	0.12	0.08	0.19	0.06	0.01	0.02

Table C13. Boundary station, 1975.

| Date | N as N (mg L^{-1}) | | | P as P (mg L^{-1}) | |
	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Total P	Dissolved ortho-P
6-06	2.1	1.1	0.08	0.15	0.04
	2.4	1.1	0.08	0.16	0.03
6-27	0.05	0.03	0.02	0.03	0.02
	0.03	0.03	0.03	0.05	0.02
7-17	0.22	0.00	0.01	0.06	0.01
	0.13	0.00	0.04	0.11	0.01
7-31	0.09	0.03	0.00	0.01	0.01
	0.25	0.00	0.07	0.04	0.04
8-15	0.16	0.00	0.01	0.03	0.04
	0.16	0.00	0.10	0.02	0.04
8-27	0.12	0.00	0.00	0.00	0.02
	0.12	0.00	0.11	0.03	0.03
9-12	0.02	0.00	0.01	0.06	0.02
	0.08	0.00	0.09	0.09	0.06
9-26	0.25	0.00	0.00	0.04	0.02
	0.10	0.00	0.05	0.07	0.05
10-08	0.11	0.01	0.01	0.05	0.02
	0.12	0.01	0.02	0.05	0.03
10-29	0.12	0.04	0.03	0.04	0.04
	0.00	0.00	0.04	0.04	0.04
Mean	0.32	0.12	0.02	0.05	0.02
	0.34	0.11	0.06	0.07	0.04
S.D.	0.63	0.34	0.02	0.04	0.01
	0.73	0.35	0.03	0.04	0.01

Table C14. Pinkham station, 1975.

Date	N as N (mg L^{-1})			P as P (mg L^{-1})	
	Total organic N	Total $NH_3 + NH_4^+$	Dissolved $NO_2^- + NO_3^-$	Total P	Dissolved ortho-P
5-07	0.11	0.14	0.18	0.12	0.01
	0.19	0.05	0.13	0.12	0.02
5-22	0.09	0.03	0.14	0.05	0.03
	0.09	0.00	0.15	0.18	0.03
6-05	3.1	1.1	0.08	0.09	0.04
	1.9	1.1	0.08	0.10	0.04
6-26	0.05	0.04	0.05	0.02	0.01
	0.12	0.04	0.03	0.05	0.03
7-15	0.13	0.03	0.01	0.04	0.01
	0.07	0.27	0.06	0.13	0.03
7-30	0.12	0.00	0.00	0.03	0.00
	0.16	0.00	0.05	0.12	0.03
8-14	0.12	0.00	0.00	0.03	0.02
	0.30	0.00	0.14	0.03	0.05
8-28	0.10	0.00	0.02	0.02	0.01
	0.21	0.00	0.15	0.05	0.04
9-11	0.21	0.00	0.00	0.05	0.02
	0.12	0.00	0.12	0.06	0.04
9-25	0.16	0.00	0.01	0.02	0.02
	0.12	0.00	0.13	0.07	0.03
10-07	0.15	0.00	0.01	0.03	0.02
	0.08	0.00	0.13	0.07	0.04
10-30	0.18	0.04	0.05	0.05	0.02
	0.28	0.00	0.07	0.06	0.03
Mean	0.38	0.12	0.05	0.05	0.02
	0.30	0.12	0.10	0.09	0.03
S.D.	0.86	0.31	0.06	0.03	0.01
	0.51	0.32	0.04	0.04	0.01

Table C15. Tenmile station, 1975.

Date	N as N (mg L^{-1})			P as P (mg L^{-1})	
	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Total P	Dissolved ortho-P
4-16	0.34	0.03	0.08	0.08	0.05
	0.46	0.01	0.10	0.08	0.05
5-05	0.12	0.03	0.08	0.10	0.07
	0.12	0.07	0.05	0.09	0.07
5-21	0.12	0.00	0.14	0.13	0.04
	0.12	0.05	0.05	0.05	0.04
6-03	0.33	0.59	0.07	0.06	0.03
	0.12	0.43	0.05	0.06	0.04
6-24	0.44	0.02	0.02	0.03	0.01
	0.39	0.00	0.10	0.05	0.02
7-14	0.38	0.00	0.21	0.03	0.00
	0.30	0.00	0.00	0.06	0.01
7-28	0.47	0.00	0.01	0.01	0.02
	0.30	0.00	0.08	0.05	0.05
8-11	0.04	0.01	0.00	0.03	0.01
	0.01	0.00	0.22	0.03	0.04
8-26	0.08	0.00	0.00	0.01	0.01
	0.08	0.00	0.19	0.05	0.03
9-09	0.08	0.00	0.01	0.04	0.01
	0.30	0.00	0.18	0.08	0.02
9-23	0.08	0.00	0.00	0.03	0.04
	0.11	0.00	0.14	0.05	0.06
10-06	0.06	0.02	0.01	0.03	0.01
	0.06	0.02	0.13	0.07	0.03
10-28	0.16	0.01	0.03	0.06	0.02
	0.16	0.01	0.12	0.08	0.04
Mean	0.21	0.05	0.05	0.05	0.02
	0.19	0.05	0.11	0.06	0.04
S.D.	0.16	0.16	0.06	0.04	0.02
	0.14	0.12	0.06	0.02	0.02

Table C16. Forebay station, 1975.

Date	N as N (mg L^{-1})			P as P (mg L^{-1})	
	Total organic N	Total NH$_3$ + NH$_4^+$	Dissolved NO$_2^-$ + NO$_3^-$	Total P	Dissolved ortho-P
4-18	0.36	0.02	0.06	0.03	0.00
	0.35	0.08	0.11	0.04	0.01
5-06	0.22	0.06	0.05	0.06	0.03
	0.14	0.08	0.07	0.10	0.05
5-20	0.04	0.02	0.06	0.04	0.01
	0.02	0.06	0.05	0.04	0.02
6-04	0.08	0.22	0.05	0.06	0.03
	0.11	0.27	0.05	0.06	0.04
6-25	0.09	0.03	0.02	0.00	0.01
	0.10	0.08	0.11	0.06	0.05
7-18	0.25	0.00	0.04	0.04	0.01
	0.12	0.00	0.14	0.06	0.03
7-29	0.05	0.03	0.00	0.06	0.00
	0.21	0.00	0.14	0.08	0.07
8-12	0.09	0.01	0.01	0.03	0.01
	0.03	0.01	0.19	0.05	0.06
8-29	0.08	0.00	0.01	0.01	0.01
	0.12	0.00	0.21	0.05	0.04
9-10	0.12	0.00	0.01	0.02	0.01
	0.12	0.00	0.20	0.07	0.05
9-24	0.08	0.00	0.00	0.03	0.01
	0.09	0.00	0.20	0.07	0.04
10-09	0.21	0.01	0.02	0.04	0.01
	0.13	0.01	0.20	0.07	0.03
10-31	0.27	0.00	0.05	0.05	0.02
	0.01	0.02	0.25	0.08	0.05
Mean	0.15	0.03	0.03	0.04	0.01
	0.12	0.05	0.15	0.06	0.04
S.D.	0.10	0.06	0.02	0.02	0.01
	0.09	0.08	0.07	0.02	0.02

APPENDIX D: PRIMARY PRODUCTIVITY IN LAKE KOOCANUSA.

a.   1972.

b.   1973.
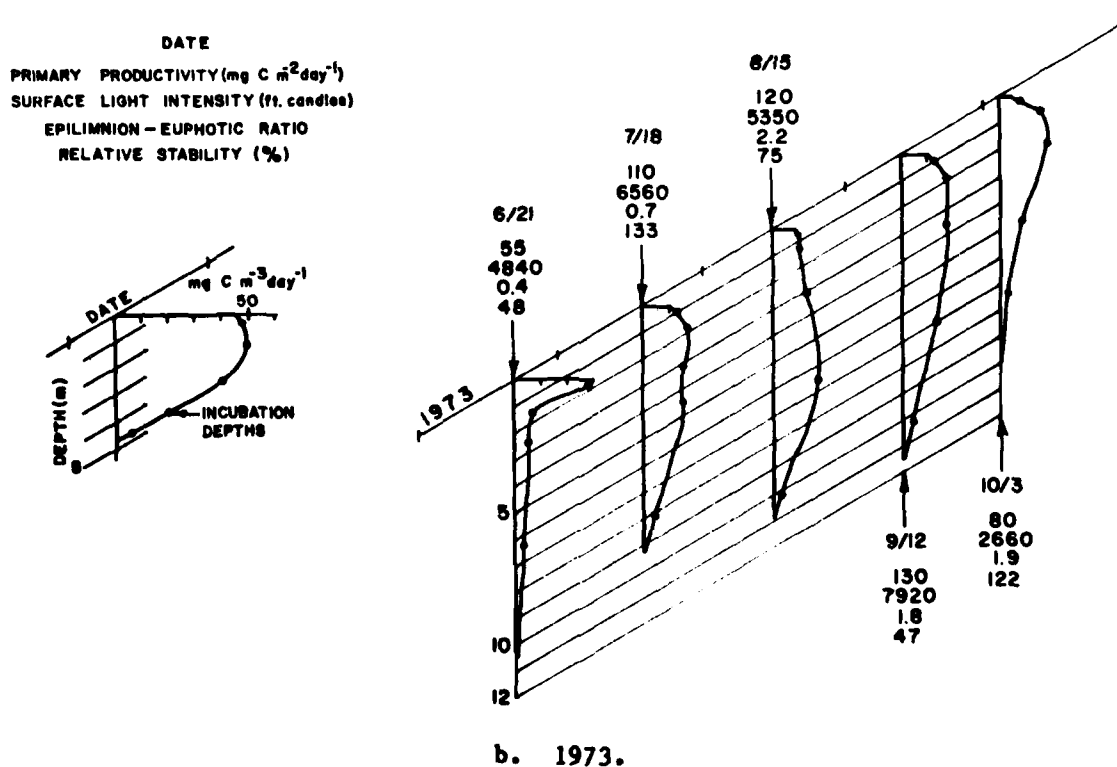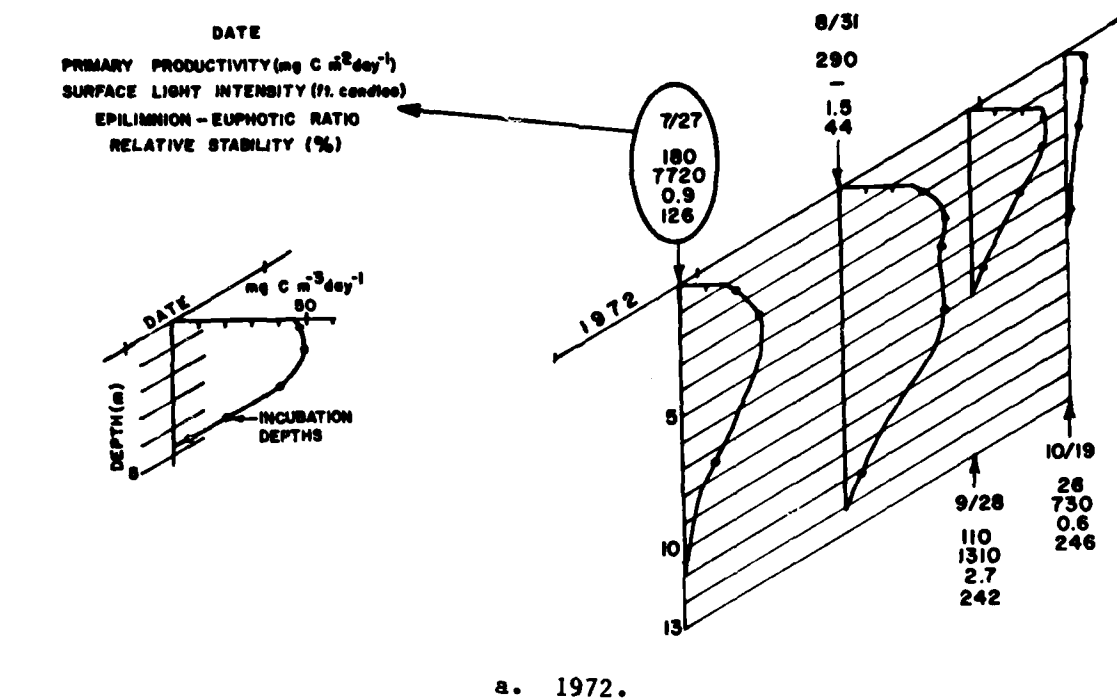
Figure D1.   In situ primary productivity in Lake Koocanusa, Boundary station.
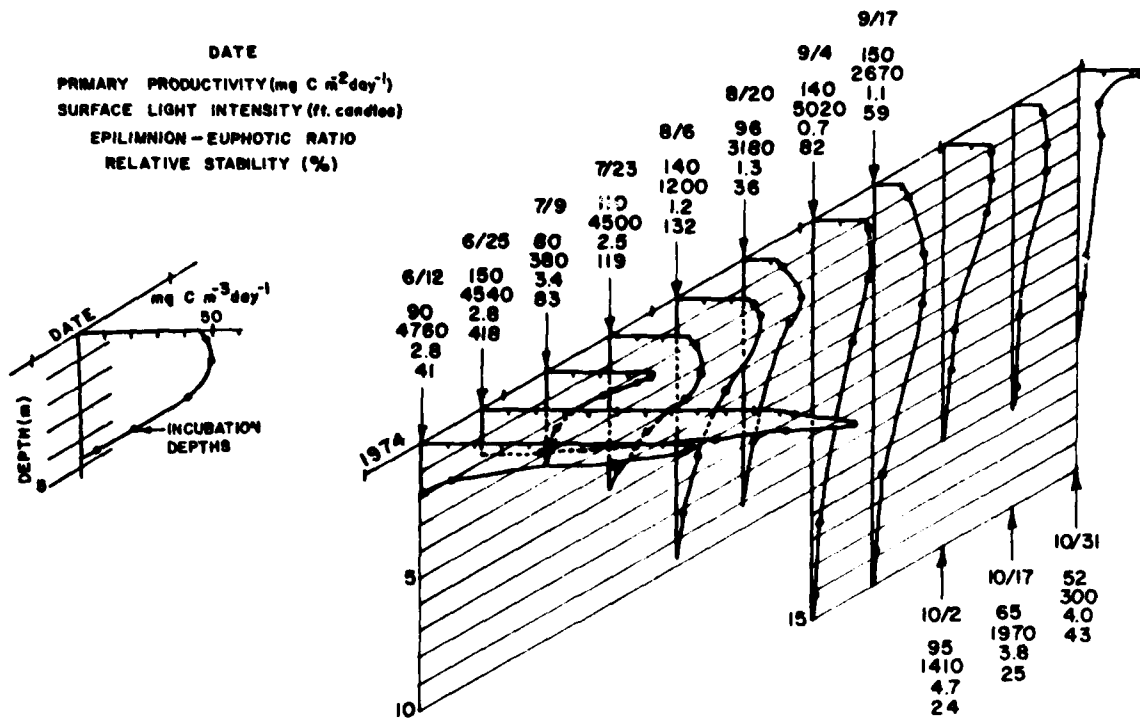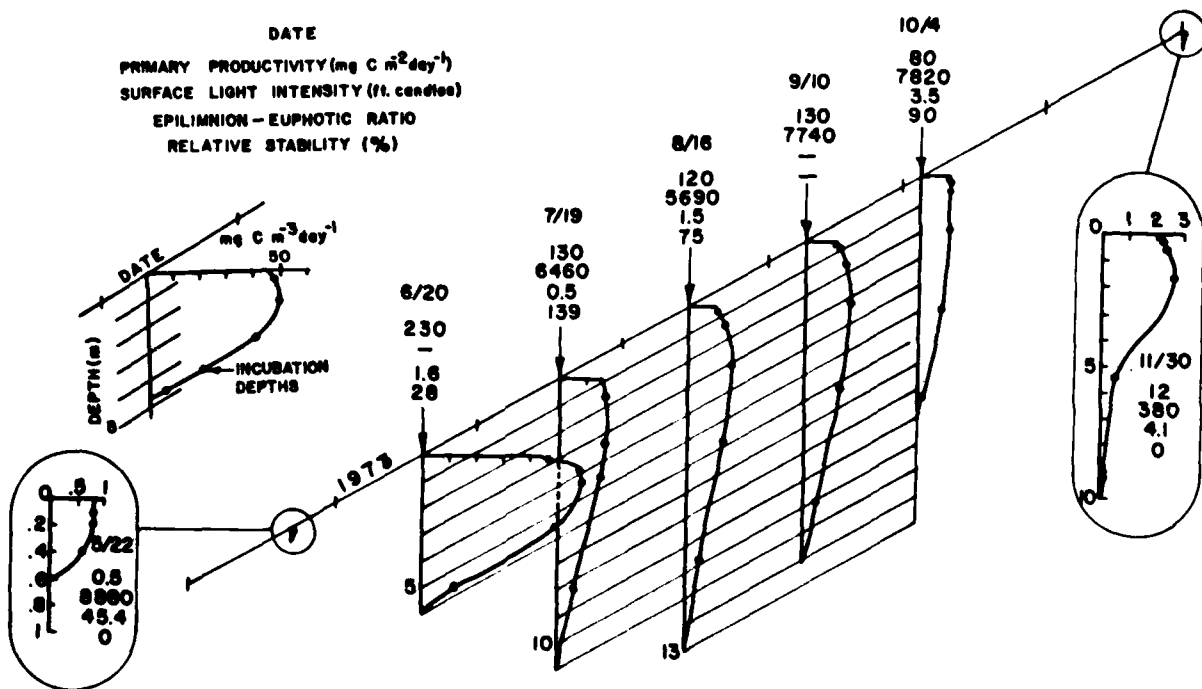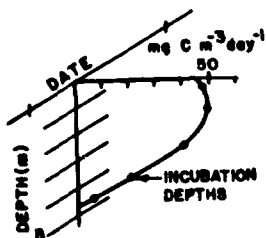
c. 1974.
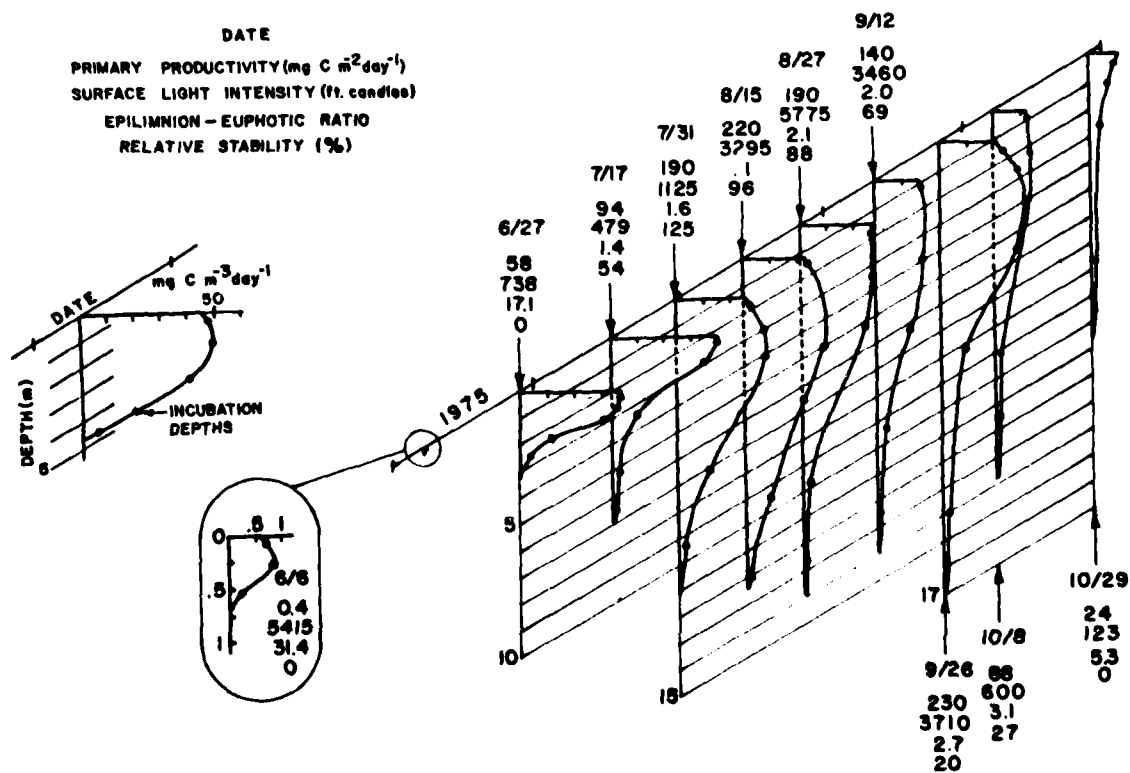
d. 1975.

Figure D1 (cont'd). In situ primary productivity in Lake Koocanusa, Boundary station.
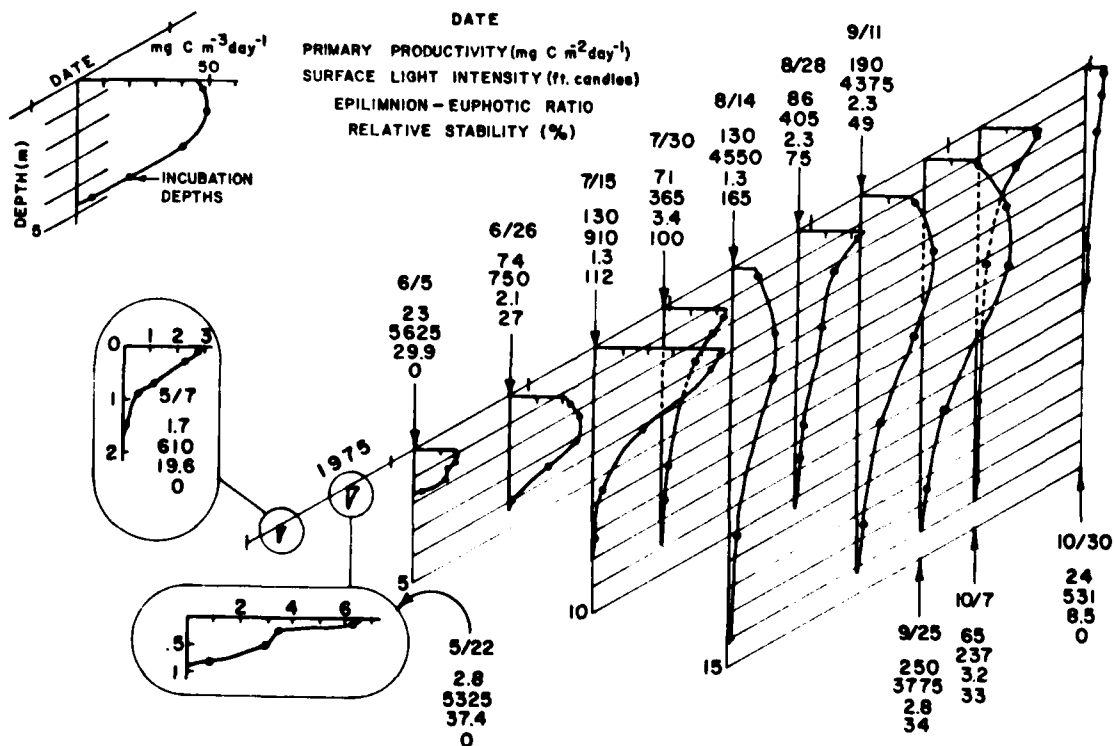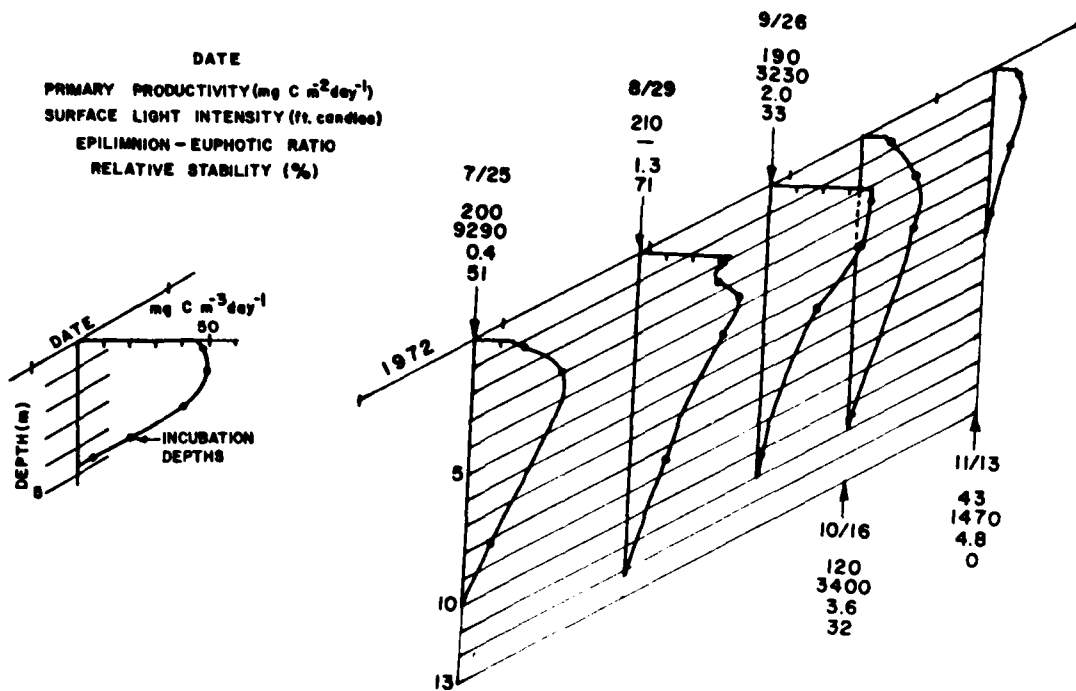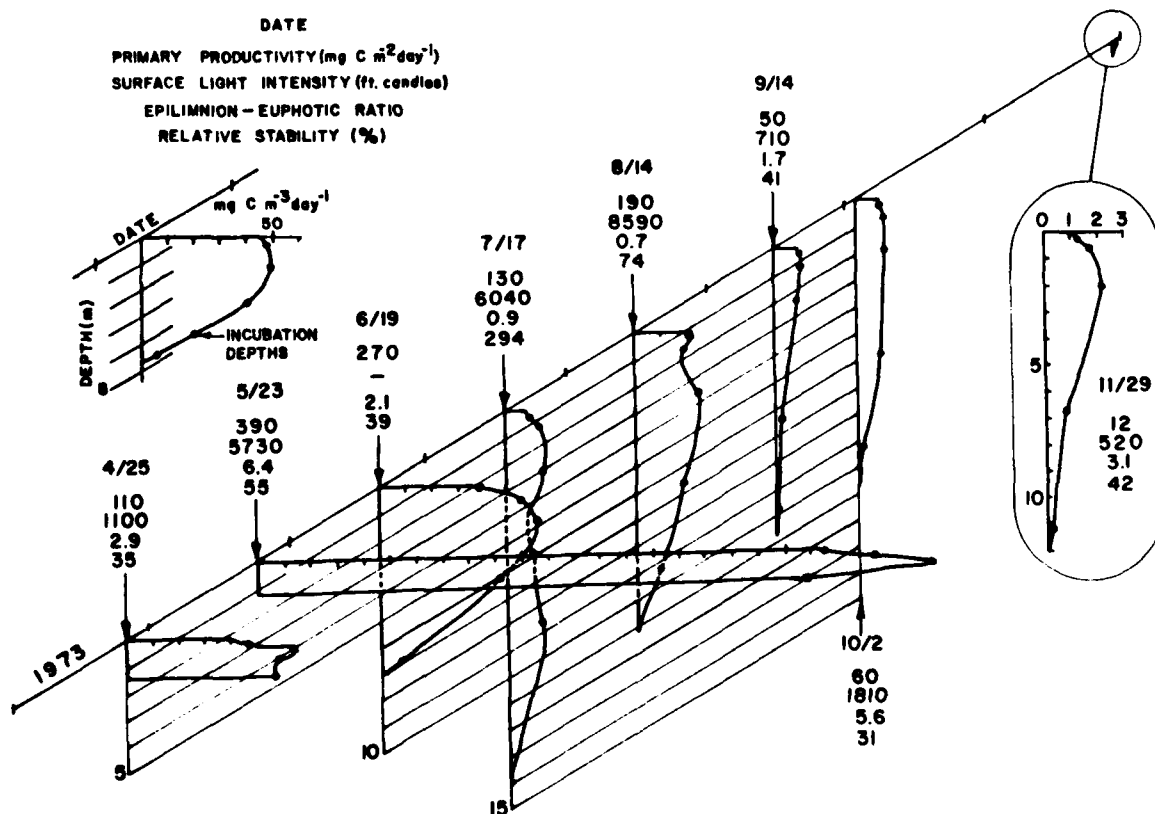
a. 1972.

b. 1973.

Figure D2. In situ primary productivity in Lake Koocanusa, Pinkham station.
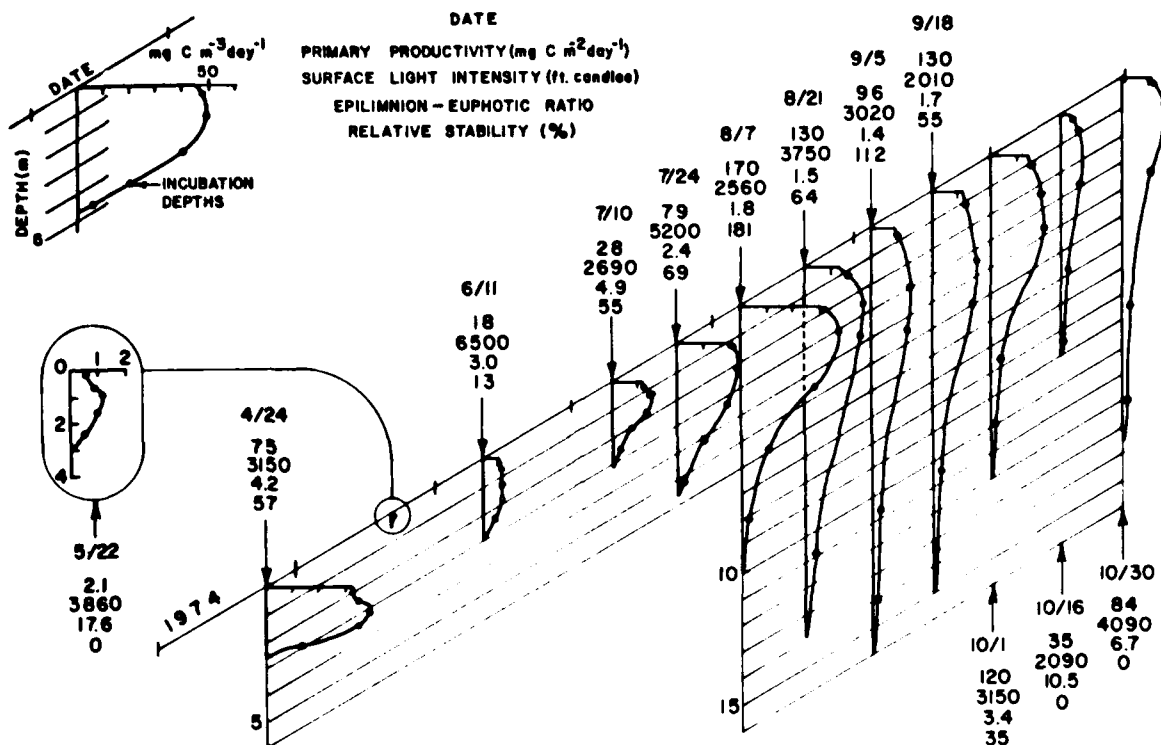
c. 1974.

d. 1975.

Figure D2 (cont'd). In situ primary productivity in Lake Koocanusa, Pinkham station.
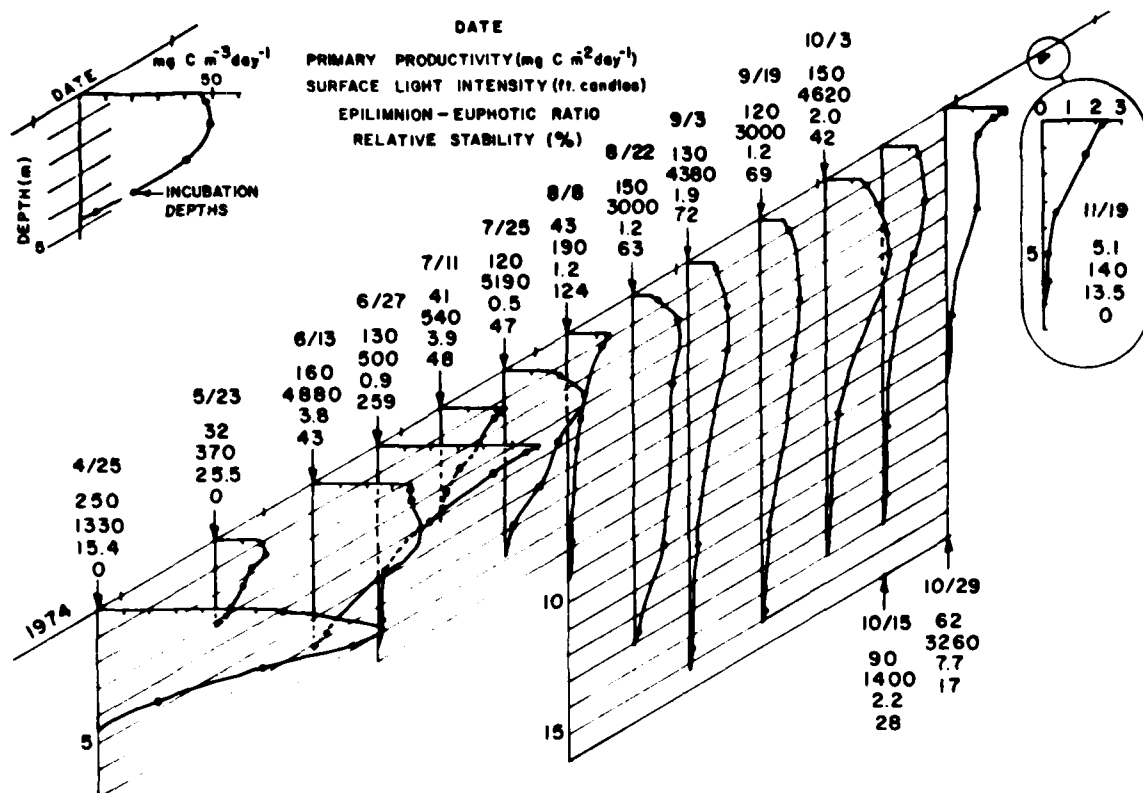
DATE

PRIMARY PRODUCTIVITY (mg C m⁻²day⁻¹)

SURFACE LIGHT INTENSITY (ft. candles)

EPILIMNION - EUPHOTIC RATIO

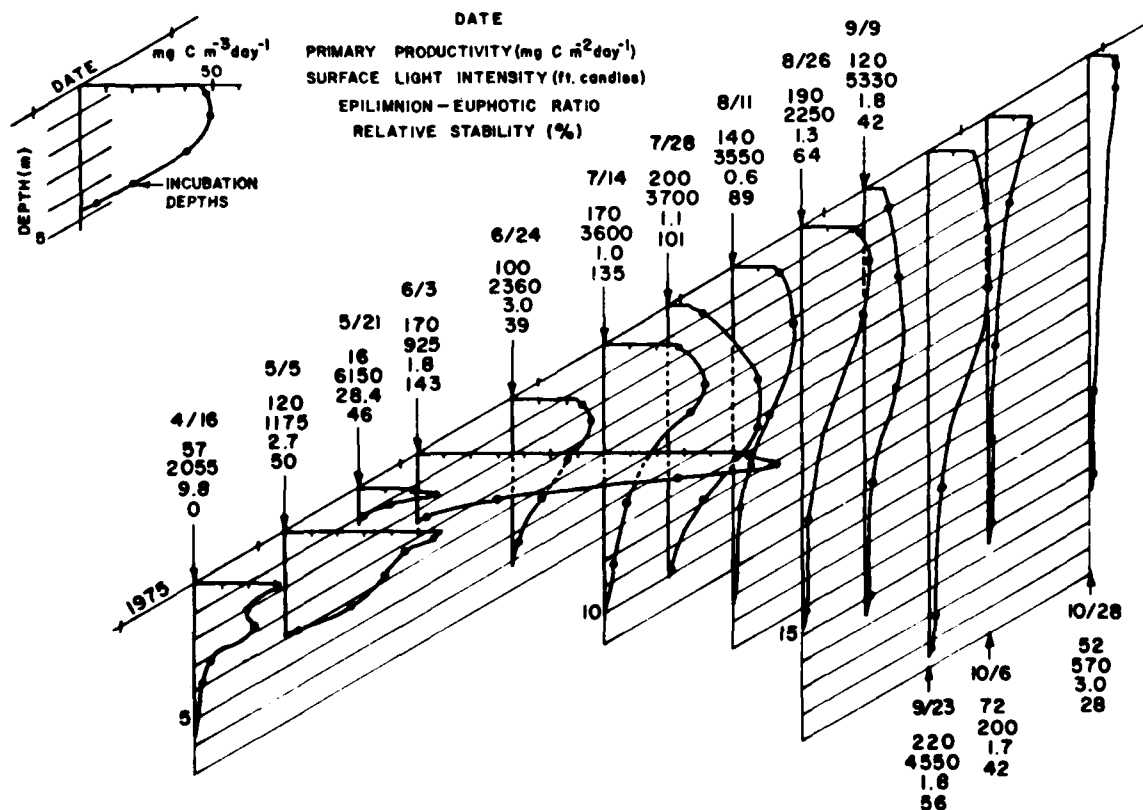RELATIVE STABILITY (%)

a. 1972.

b. 1973.

Figure D3.   In situ primary productivity in Lake Koocanusa, Tenmile station.

c. 1974.

d. 1975.

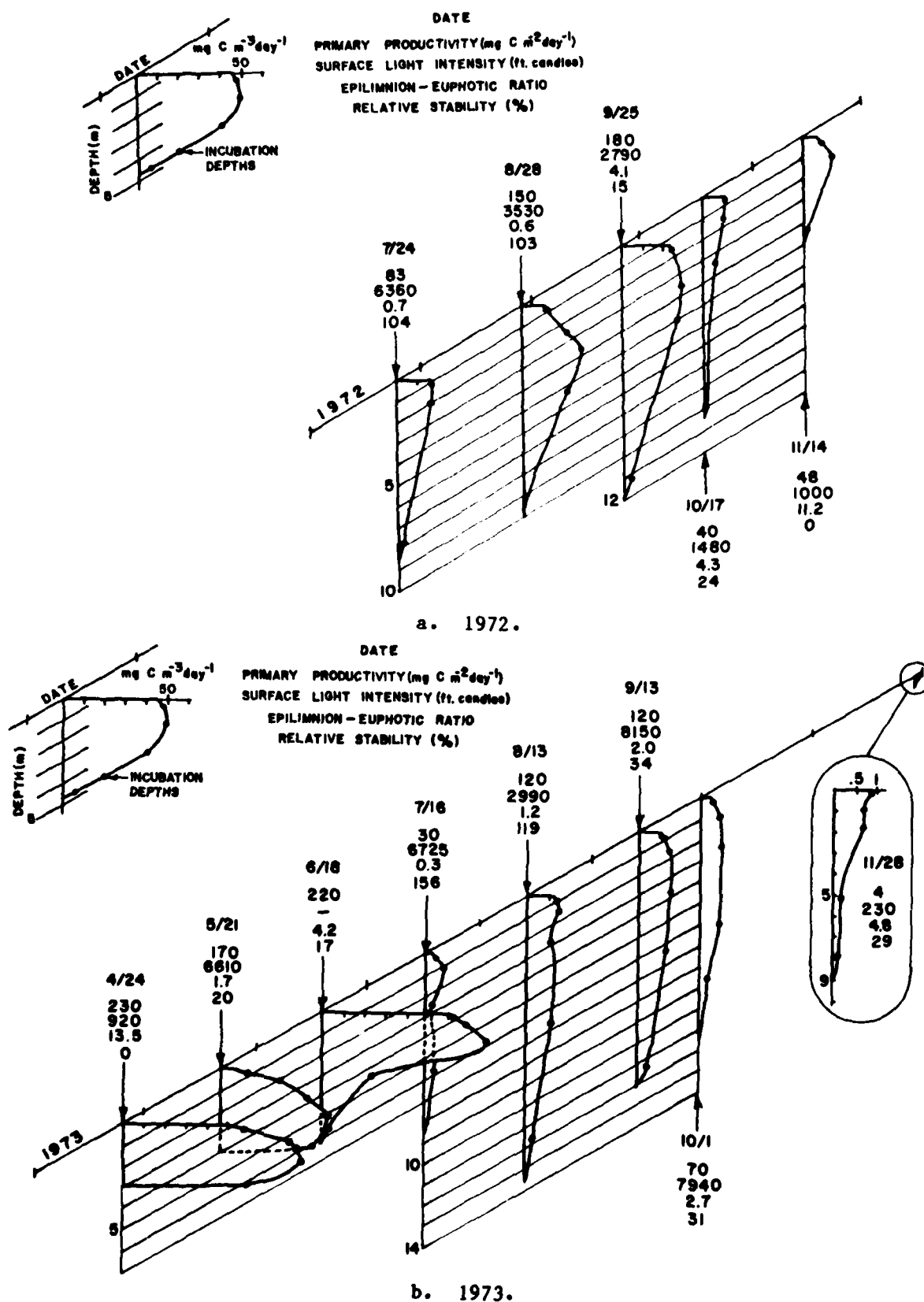Figure D3 (cont'd). In situ primary productivity in Lake Koocanusa, Tenmile station.
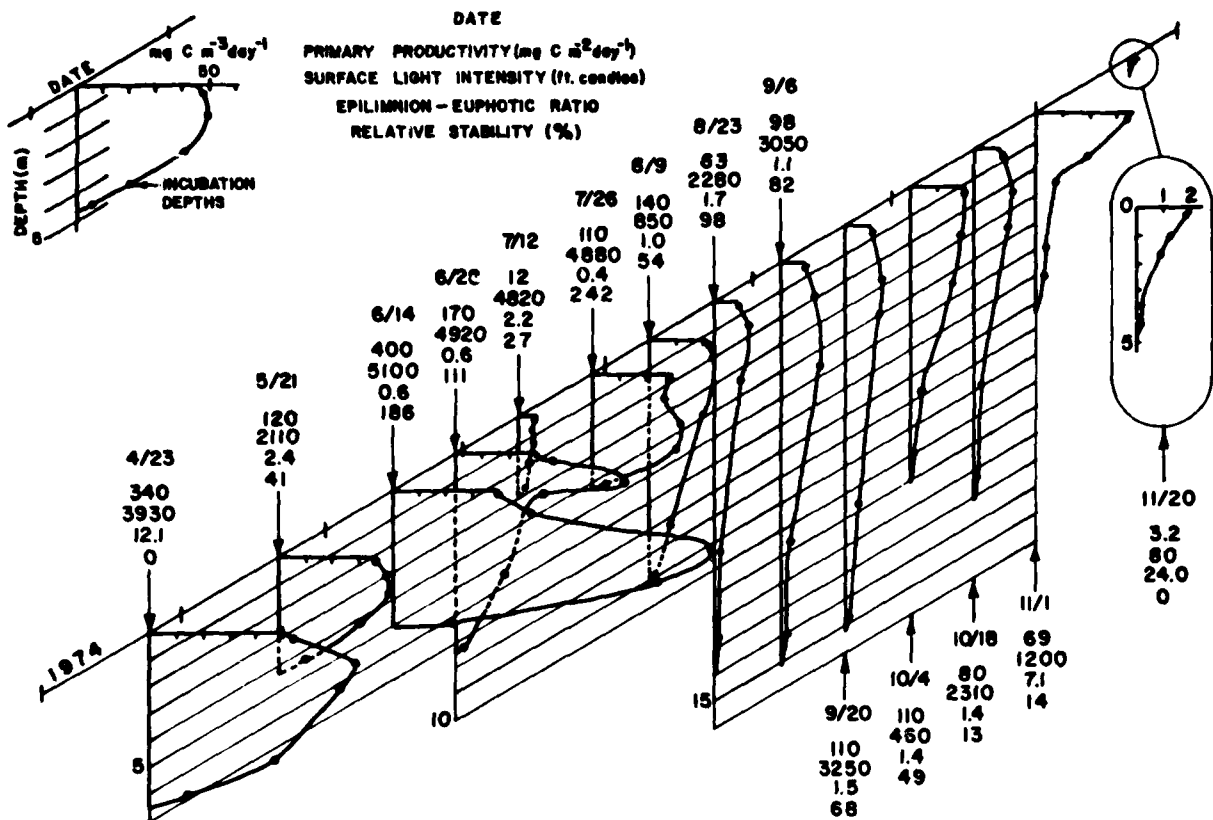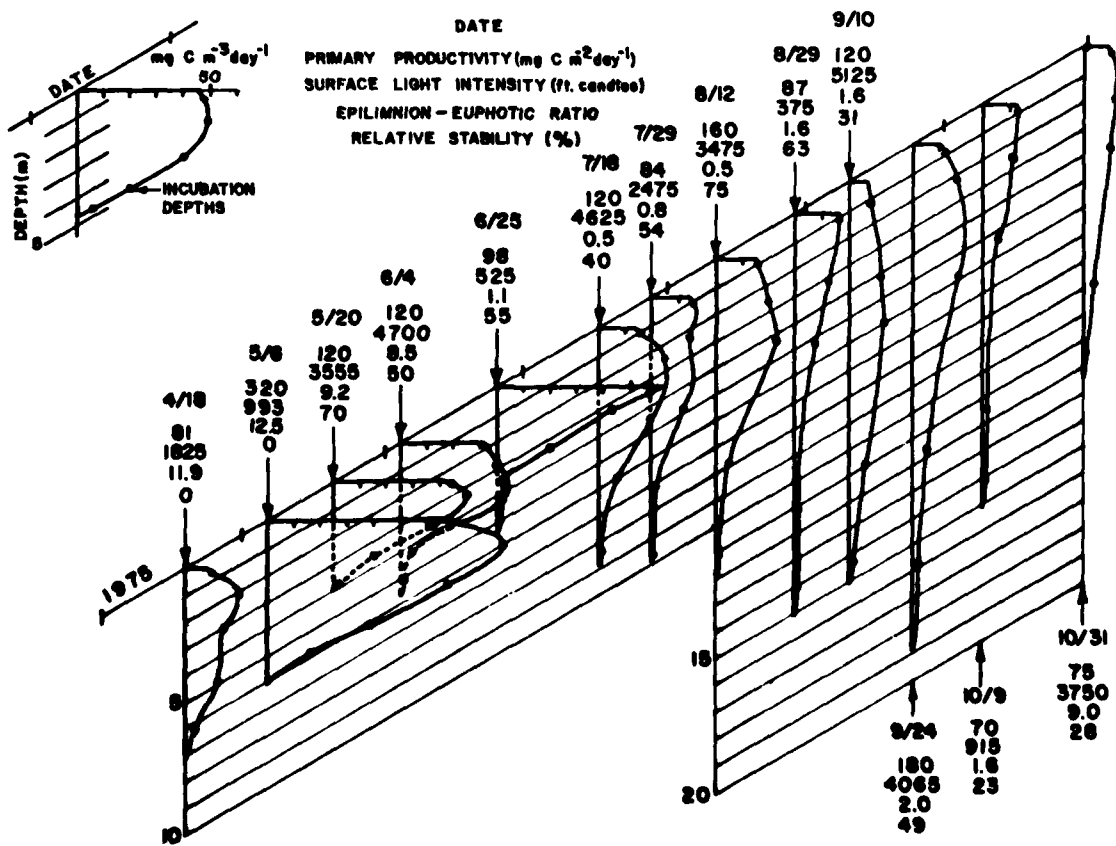
104

DATE
PRIMARY PRODUCTIVITY (mg C m⁻² day⁻¹)
SURFACE LIGHT INTENSITY (ft. candles)
EPILIMNION – EUPHOTIC RATIO
RELATIVE STABILITY (%)

a.   1972.

DATE
PRIMARY PRODUCTIVITY (mg C m⁻² day⁻¹)
SURFACE LIGHT INTENSITY (ft. candles)
EPILIMNION – EUPHOTIC RATIO
RELATIVE STABILITY (%)

b.   1973.

Figure D4.   In situ primary productivity in Lake Koocanusa, Forebay station.

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c. 1974.

d. 1975.

Figure D4 (cont'd). In situ primary productivity in Lake Koocanusa, Forebay station.

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DATE
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